Large-scale forcing of coastal communities.

Thesis

Large-scale forcing of coastal communities

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Richard Shelmerdine

Abstract

Two contrasting areas of pelagic primary productivity (PPP) were noted in western Scotland, the Clyde (high PPP) and the west coast (low PPP). It was hypothesised that increased PPP would have a direct bottom-up influence on intertidal community structure with the Clyde expected to be dominated by filter feeders with potentially greater larval recruitment, increased density, faster growth and larger maximum sizes.

The study was divided into five sections examining community structure, growth rates, predation and grazing pressures, effects of wave exposure, and stable isotope analysis. Individual species tended to vary between sites within lochs rather than between the two regions.

Growth rates of the predator *Nucella* were found to follow peaks in *Semibalanus* size, rather than *Mytilus*, with increased growth on the west coast. An increased density of the grazer, *Littorina*, at a site had an increased effect on their growth rate although dense localised patches within sites were observed where growth rates were lowest. Mussel size classes were found to have different growth rates, most probably due to differing factors such as predation, food availability, and reproduction.

Predation and grazing effects differed between regions. Barnacle cover was shown to be affected by both *Nucella* and *Littorina* although the latter may have been an indirect affect due to the biofilm cover which was greater in the Clyde. Predation rates of mussels were found to be greater on the west coast which was most probably due to a change in diet from barnacles to mussels.

Mussel shell length and biomass declined with increasing wave exposure throughout western Scotland with the potential for factors varying on small scales to be more important in structuring mussel populations.

This was evident when testing for differences in stable isotopes of mussels which suggested site specific variation due to increased freshwater input.

The results of this study showed that small scale, local factors are as important, if not more, as regional differences in structuring communities. PPP is important, but only for a subset of the community.

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Although many months were spent in front of a computer screen carrying out what seemed like an endless number of various analyses which culminated in this written manuscript, none of this would have been possible if it were not for the many people that accompanied me, taking time out of their own busy schedules, on my various field trips to collect my data. In particular Linda Robb, Robin Harvey, and Jenny Beaumont who all voluntarily helped me on more than one occasion. I still wonder if you were all gluttons for punishment or interested in my work. I like to think it was the latter and thank you most sincerely for your help.

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Chapter 1 General Introduction

Marine intertidal communities and their associated species have been extensively studied over the years examining varying aspects of the life histories of intertidal species in relation with biotic and abiotic factors over varying spatial scales. Studies up to the 1960s focussed on intertidal community structure (for examples see Kitching 1935; Stephenson and Stephenson 1949; Lewis 1956; Lewis and Powell 1960b) with specific reference to species settlement (Knight-Jones and Stevenson 1950; Knight-Jones 1953), distribution (Crisp 1950; Powell 1954; Southward and Crisp 1954, 1956; Crisp and Southward 1958; Lewis and Powell 1960a), growth rates (Barnes 1956; Crisp 1960; Patel and Crisp 1960), and breeding (Crisp 1950; Crisp and Davies 1955). During the mid 1950s Crisp and co-authors investigated abiotic influences, in particular water flow (Crisp 1955), and the type (Crisp and Davies 1955) and contour (Crisp and Barnes 1954) of the substrate, while the importance of exposure was recognised as a significant influencing factor on intertidal communities (Lewis 1954). Biotic interactions, such as predation and interspecific competition, were recognised in the late 1950s and early 1960s (see Kitching *et al.* 1959; Connell 1961b, 1961a). The majority of these studies focussed on small, local scale variations and it was not until the mid 1960s onwards when variation in species' life history parameters were examined in relation with much larger scale processes such as supply-side ecology (Bayne 1964), effects of climatic change on species abundances (Southward 1967), and pelagic food availability (Foster-Smith 1975). The introduction of ecological concepts such as supply-side ecology, the intermediate disturbance hypothesis, and patch dynamics in rocky intertidal habitats were reported from the mid 1960s through to the mid 1980s. It was not until the early 1990s (for examples see Farrell *et al.* 1991; Hunter and Price 1992; Menge 1992) when large-scale oceanographic conditions were considered to be a significant driving force, at a smaller scale, in structuring intertidal rocky shore communities. The determination of community patterns can be controlled by either top-

down or bottom-up driven processes (for review see Menge 2000). Bottom-up control is when community patterns are determined by the supply of food or nutrients (Menge 1995) while top-down communities are said to be controlled by predation or grazing/herbivory which sets the abundance or biomass of lower trophic levels (for examples see, Menge 1995; Menge *et al.* 1997b; Menge *et al.* 1997a; Leonard *et al.* 1998; Menge *et al.* 1999; McQuaid and Lindsay 2000; Nielsen 2001; Sanford and Menge 2001; Dulvy *et al.* 2002; Gratton and Denno 2003; Methratta 2004).

1.1 Oceanographic Processes

"The general assumption among benthic marine researchers was that oceanographic conditions were more or less homogeneous over scales of 100s to 1000s of kilometres and thus less likely to have any influence in underlying variation in community structure and dynamics" (Menge *et al.* 2002). Remote sensors, such as satellite imaging systems, often revealed striking and consistent variation in oceanographic conditions (e.g. SST, chlorophyll) associated with specific coastal areas, suggesting the alternative view that such variability may have important ecological consequences in coastal benthic environments (Menge *et al.* 2002). This variation in near shore oceanography can generate alongshore differences in phytoplankton productivity, rates of larval transport and delivery, and macrophyte production (Menge 2003). Large-scale, long-term changes can dominate variation in abundance and community composition and are thought to be associated with oceanographic processes (Shanks 1983; Caffey 1985; Dayton *et al.* 1999).

1.1.1 Previous studies examining the effects of large-scale oceanographic conditions on small-scale intertidal community structure

Many studies have looked at intertidal community structure in relation to top-down driven effects (such as the effects of grazing and predation) but only fairly recently have bottom-up effects (food supply) been shown to be relevant within the intertidal (for review see, Menge 2000). Areas of contrasting primary production such as those found in Chile (Wieters *et al.* 2003; Nielsen and Navarrete 2004; Lagos *et al.* 2005), California (Dayton *et al.* 1999), Oregon (Menge *et al.* 1997b; Menge *et al.* 2002), and New Zealand (Menge *et al.* 1999; Menge *et al.* 2002) have shown the main driving forces of intertidal community structure within these areas to be bottom-up related (food supply and temperature). These bottom-up processes were governed by differing environmental gradients such as a varying upwelling intensity in Oregon, differing oceanographic regimes of upwelling versus downwelling in New Zealand, and the nutrient poor El Niño versus the nutrient rich La Niña of Chile and California. Varying upwelling intensity affected phytoplankton productivity, and detritus and nutrient concentrations (Menge 2000). Menge *et al.* (2002) showed that there was sufficient variation within an upwelling regime, occurring at spatial scales of 10s to 100s of kilometres, to underlie significant among site variations along the Oregon coast. Studies of a similar nature have been carried out in South Africa (Menge 1995; Bustamante and Branch 1996b, 1996a; McQuaid and Lindsay 2000) although the scale of variability is much larger in this area with intertidal communities on the east coast being more representative of a tropical shore while those on the west coast being more temperate.

1.1.2 Oceanographic processes in western Scotland

The western shores of Scotland consist of an intricate and complex system of fjord-like sea lochs. It has been found, from average satellite data (courtesy of NASA, Sea-viewing Wide Field-of-View Sensor (SeaWiFS) onboard the OrbView-2 spacecraft), that the Clyde system has a higher level of pelagic primary productivity compared to that of the west coast (Figure 1.1 to Figure 1.3). For the purposes of this study the west coast refers to the west coast of Kintyre and northwards past the Isle of Skye to Tongue in the north (the area to the left of the dashed line in Figure 1.1) and the Clyde system to the complex combination of the Clyde Sea (found to the east of Kintyre encompassing the Isle of Arran and the Island of Bute) with its associated sea lochs (the boxed area in Figure 1.1). Average surface chlorophyll *a* concentrations were found to be similar from 1999, 2000, and 2001 (Figure 1.2a to Figure 1.2c, respectively) with each year composed of roughly 200 images. On a finer scale, each pixel is an average of 40 to 50 satellite images, although this number declines with proximity to the coast, and have a resolution of 1.1 km (Figure 1.3). Although areas of high averaged pelagic primary productivity are present on the west coast, these concentrations are not found within loch systems as is the case for the lochs in the Clyde system (Figure 1.3).

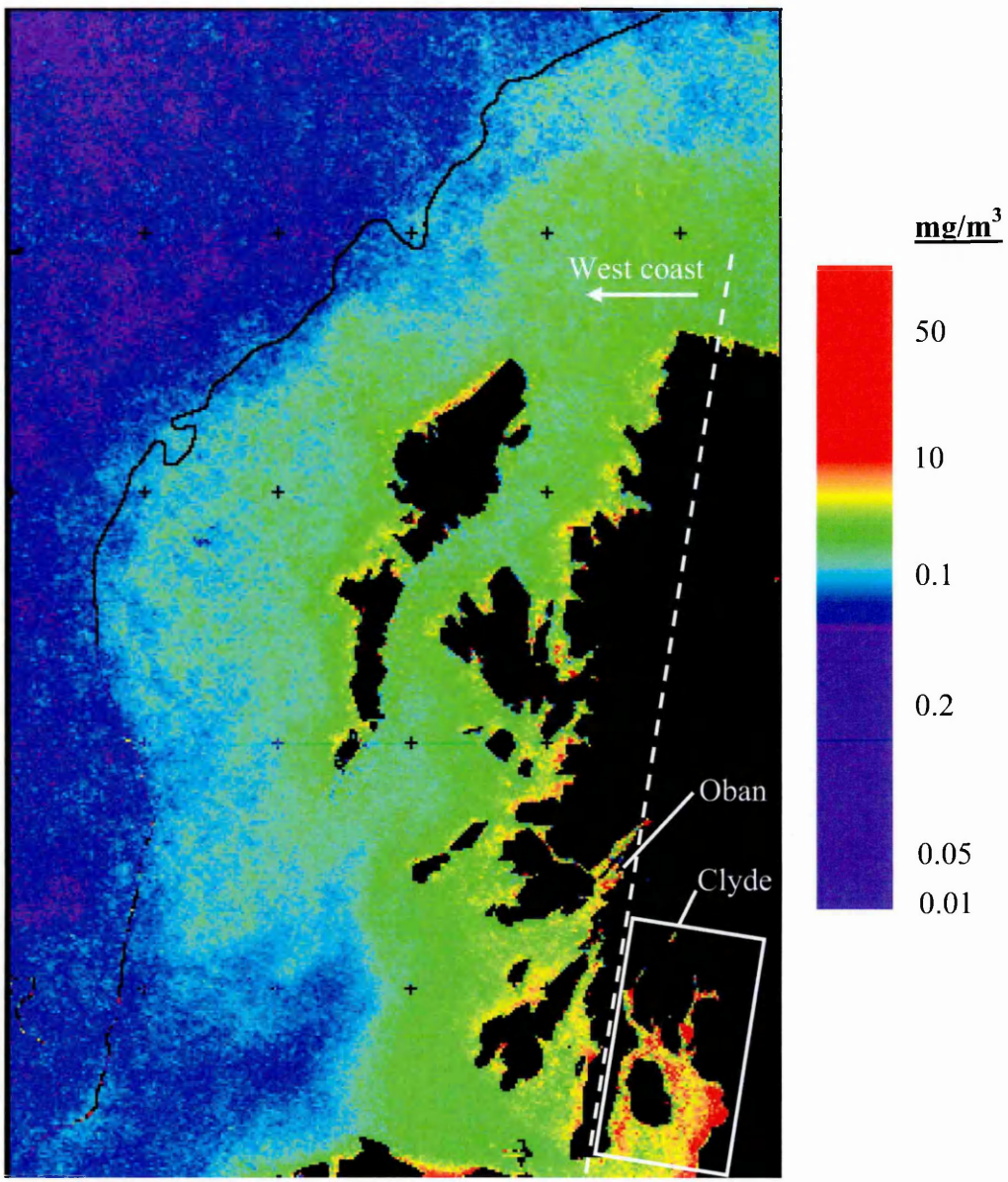


Figure 1.1 Average surface chlorophyll *a* concentrations around western Scotland from 2001. Data obtained from the SeaWiFS satellite courtesy of NASA. Concentrations have been altered from grey scale to false colour. The Clyde (boxed area) and the west coast (area to the left of the dashed line) are shown.

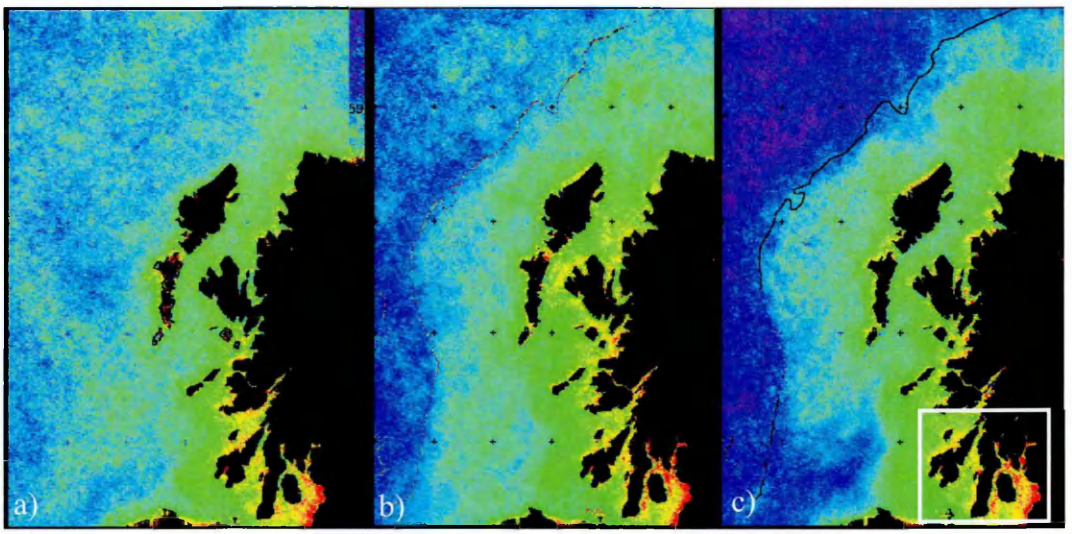


Figure 1.2 Average surface chlorophyll *a* concentrations around western Scotland from 1999 (a), 2000 (b), and 2001 (c). See Figure 1.1 for details of concentrations.

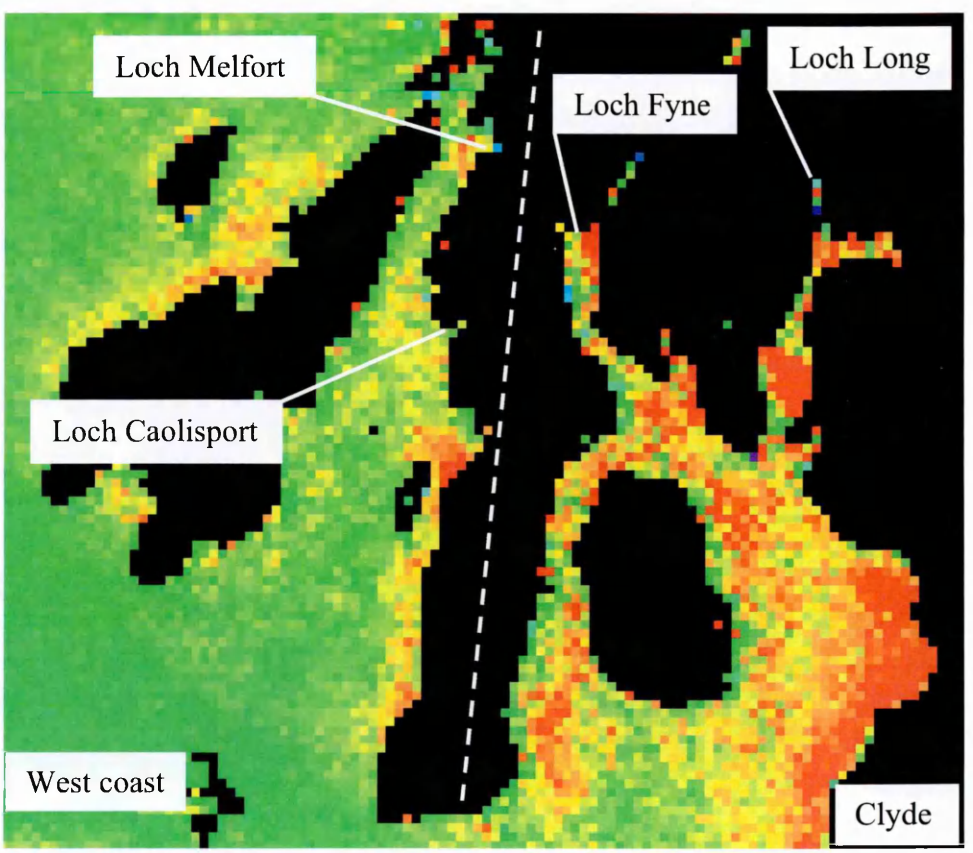


Figure 1.3 Average surface chlorophyll *a* concentrations from the boxed area marked in Figure 1.2c. The locations of four lochs, Lochs Fyne and Long in the Clyde and Lochs Melfort and Caolisport on the west coast, are shown. The dashed line denotes the separation between the west coast and the Clyde. See Figure 1.1 for details of concentrations.

1.1.3 Clyde system and its oceanographic processes

Much work has been carried out on the hydrography of the Clyde Sea and its associated sea lochs (Edwards *et al.* 1986; Tett *et al.* 1986; Grantham and Tett 1993; Matthews *et al.* 1999; Bowers *et al.* 2000; Tett *et al.* 2003) with Edwards *et al.* (1986) describing the hydrography in relation to the benthic topography. Edwards *et al.* (1986) considered the Clyde system as a vast fjord, the largest in Scotland, with both the sea and lochs showing a reduction in surface salinity, a summer thermocline, eventual renewal of summer stagnant bottom water by density currents, and fronts on the shallow loch entrance sills. The Great Plateau (<50 m deep) at the entrance to the Clyde Sea separates the well mixed water of the North Channel with stratified waters within the Clyde system (Edwards *et al.* 1986). The residence time of surface waters in this area was found to be about two months which was due to an exchange with the North Channel of about 1.6×10^4 m^3 s^{-1} (Edwards *et al.* 1986; Grantham and Tett 1993; Matthews *et al.* 1999; Tett *et al.* 2003). This slow exchange may account for the higher levels of pelagic primary productivity found in the Clyde system which is backed up with the study by Tett *et al.* (1986) which found a significantly greater monthly maximum chlorophyll concentration in Loch Striven (a Clyde loch) to that of Loch Creran (a west coast loch) although no difference was found when examining median concentrations.

1.1.4 Scottish west coast and its oceanographic processes

The hydrography and oceanography of the west coast of Scotland has been well documented (Tett and Wallis 1978; McKinley *et al.* 1981; Ellett and Edwards 1983;

Gowen *et al.* 1983; Jones *et al.* 1984; McKay *et al.* 1986). Although this area covers a much larger spatial scale than that of the Clyde system, work on similar latitudes in the Sound of Jura (Jones *et al.* 1984) and slightly further north in the Firth of Lorn (Wood *et al.* 1973; Tett and Wallis 1978; Gowen *et al.* 1983) have been carried out. As a result of close proximity to an amphidromic point, i.e. a position where the tidal range is inappreciable, all the tides in south-western Argyll are of small range (Lewis and Powell 1960a). This can be seen in the Sound of Jura where a very small spring tide range (only 0.6 to 1.2 meters) is found, which results in a very compressed littoral zone, especially at sites sheltered from wave-action (Lewis and Powell 1960b). With neap tides fluctuating only to a small extent around mid tide level (MTL), the loch shores can be divided roughly into two major zones of which the upper one will theoretically be submerged only at spring tides (Lewis and Powell 1960a). In the north of the Sound the mean spring tidal range increases to about two meters (Jones *et al.* 1984). Lochs within this area have a much higher flushing rate, compared to the Clyde system, of five to eight days and although frontal regions occur within the Sound their contribution to the overall production within the area is likely to be low because of their small size and slight enhancement of phytoplankton standing crop (Jones *et al.* 1984).

1.2 Phytoplankton

The lowest trophic level of the majority of intertidal food webs consists of phytoplankton. Variation in phytoplankton abundance impacts higher trophic levels which in turn affects the structure of the intertidal community. Prins *et al.* (1996) observed lower chlorophyll *a* concentrations, which is known to provide a good estimate of phytoplankton biomass (Methratta 2004), during ebb than during flood tides within an estuary. Filter feeders may reduce phytoplankton concentration (Archambault

et al. 1999) which is considered to be a high-quality food source (Page and Lastra 2003). Sites of consistently higher concentrations of phytoplankton appear to have greater rates of recruitment and growth of sessile suspension feeders (Sanford and Menge 2001) while rates of grazing and predation also appear to be higher at these sites (Menge 1992; Menge *et al.* 1997b). Filter feeders, such as barnacle and mussel species, are the most likely component of intertidal community assemblages to respond to changes in phytoplankton availability. High phytoplankton abundance has been found to support increased filter feeder growth with a potential reduction in macrophyte abundance through competition for space (Menge *et al.* 1999). When macrophyte abundance was low, the abundance of filter feeders, macro-herbivores (limpets, chitons), and predators (sea stars, whelks) were high (Menge *et al.* 1997b) and vice versa.

While various authors have studied intertidal community structure in these two areas in the past, particularly in the Clyde at Millport (Chthamalus stellatus (Poli, 1791) distribution Connell 1961b; growth of Semibalanus balanoides (L., 1767) and Balanus crenatus Brugiere, 1789 Barnes and Powell 1968) and along the west coast of Scotland (see, Kitching 1935; Lewis 1954, 1956; Lewis and Powell 1960b, 1960a; Burrows *et al.* 2002), none have ascribed regional differences to primary productivity.

1.3 Aims of this study

The overall aim of the study was to test whether differences in the structure and functioning of intertidal communities exist between two areas of contrasting primary productivity.

H_0 = No variation in intertidal community structure will be observed between areas of large scale variation in pelagic primary productivity.

To test the null hypothesis the study was divided into five sections.

These sections tested differing, but interlinked, hypothesis in order to establish how large-scale oceanographic processes affect intertidal community structure in western Scotland (Figure 1.4). An initial broad scale survey was followed by continuous monitoring of populations and communities in small areas at specific locations within regions of differing pelagic primary productivity (Chapter 2). Permanent monitoring plots were established and areas cleared to test for differences in species colonisation rates and their intensity with further image analysis conducted examining barnacle growth, settlement, and mortality rates. The primary aim of Chapter 2 was to investigate whether community structure and species composition differ between areas of high and low pelagic primary production. It was hypothesised that the west coast, an area of low pelagic primary production, would be dominated by macroalgae and the Clyde, an area of high pelagic primary production, would be dominated by large filter feeders.

The predicted increase in large filter feeders in the Clyde led to the hypothesis that filter feeder growth rates, and the growth rates of their corresponding predators, would be greater in this area with an increased growth rate of gastropod grazers found in the macroalgal dominated west coast. For this reason, variation in growth rates (Chapter 3) of *Nucella lapillus* (L., 1758), *Littorina littorea* (L., 1758), *Mytilus edulis* (L., 1758), and *Patella vulgata* (L., 1758) were examined. Mark-recapture experiments were conducted with the gastropod snails, *Nucella* and *Littorina*, while a more complex experimental setup involving transplantations and translocations was applied to *Mytilus* growth. Images from Chapter 2 were utilised, in conjunction with image analysis programmes, in order to determine growth in the limpet, *P. vulgata.*

The predicted increase in macroalgae on the west coast and filter feeders in the Clyde would have a corresponding increase in rates of grazing and predation, respectively. Enclosure experiments were implemented to test for any predation and grazing pressures caused by *N. lapillus* and *L. littorea* on barnacle densities (Chapter 4) at the sites established in Chapter 2. These were short term experiments which included direct measurements of predation rates of *N. lapillus* on varying size classes of *M. edulis*. It was hypothesised that predation would be greatest in the Clyde with a greater grazing influence on the west coast due to an increased food source within these areas.

As well as predation, grazing, and growth rates, abiotic factors such as wave exposure and freshwater influences would be expected to play a significant role in structuring intertidal communities. Mussels were sampled over a larger spatial scale with varying degrees of wave exposure (Chapter 5) examining variation in size and biomass. Mussel size and weight were not expected to be homogenous over a wave exposure gradient but there was no evidence from the literature to suggest whether *M. edulis* at wave exposed

sites would be large or small in shell length or biomass. The size structure of *M. edulis* populations was assessed at 55 sites from contrasting wave exposures along the shores of western Scotland. The coast was divided up into four spatially dissimilar areas which were analysed separately.

A pilot study tested for differences in stable isotope signatures of *M. edulis* over large (between lochs) and small (closeness to a freshwater source) scales (Chapter 6). Mussels which were found at wave exposed sites at the mouth of lochs were predicted to have a diet derived from a marine pelagic source while those found at wave sheltered sites within loch systems were predicted to have a diet which was heavily influenced from terrestrial sources such as land run off from freshwater sources. Since it was not possible to analyse all the samples collected in Chapter 5, a new experimental design was implemented which tested for differences in stable isotope signatures in relation to the closeness of a freshwater river source. Mussels sampled beside the river mouth were expected to have different stable isotope signatures than those sampled at least 200 meters from the river mouth. Differences would be expected to be due to terrestrial influences.

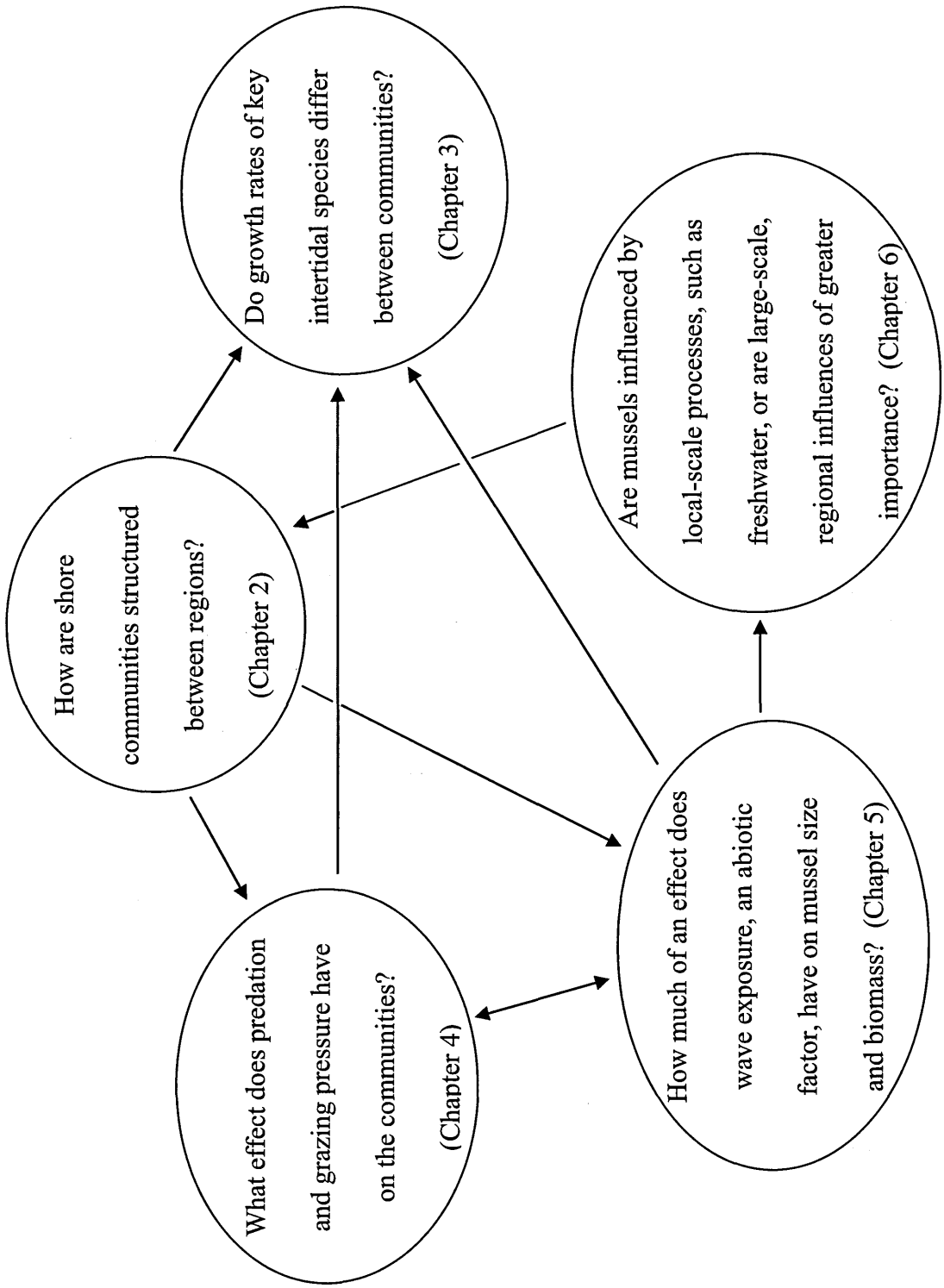


Figure 1.4 A diagrammatic representation of how the major questions from each chapter link together in order to test the effect of large-scale oceanographic processes on the community. Arrows represent the flow of information between sections.

Chapter 2 Colonisation and community structure of intertidal rocky shores in western Scotland

2.1 Introduction

It has been found, from average satellite data (Figure 1.1 to Figure 1.3), that the Clyde area has a higher level of pelagic primary productivity compared to the west coast. Filter feeders, such as barnacle and mussel species, are ideal in determining the effects that such concentrations may have on community assemblages with regard to species composition, density, and size. High phytoplankton abundance has been found to support increased filter feeder growth with a potential reduction in macrophyte abundance through competition for space (Menge *et al.* 1999). When macrophyte abundance was low, the abundance of filter feeders, macro-herbivores (limpets, chitons), and predators (sea stars, whelks) were high and vice versa (Menge *et al.* 1997b).

Studies examining species recruitment in rocky intertidal habitats with respect to community disturbance are widespread but it is only fairly recently that recruitment has been examined with regard to large scale oceanographic conditions (see Menge *et al.* 1997b; Dayton *et al.* 1999; Menge *et al.* 1999; Menge *et al.* 2002; Wieters *et al.* 2003; Nielsen and Navarrete 2004; Lagos *et al.* 2005).

2.1.1 Impact of disturbances on species succession and community structure

Disturbance in the intertidal is usually considered as the removal or clearance of patches of attached species through direct physical impacts caused naturally, through excessive wave action, ice and sediment scouring, and wave-borne debris. The effects on community structure are often short lived with the system recovering to an

approximation of the initial state (Dye 1998). Exceptions do exist and are dependent on the initial composition of the community and size of the disturbance event which may lead in a shift to an alternate state (see Petraitis and Dudgeon 1999; Petraitis and Latham 1999; Petraitis and Dudgeon 2005 for an analysis of a community shift from *Ascophyllum* to mussel and *Fucus* beds). The degree of recovery will be influenced by factors such as the time of the year that the disturbance took place, local environmental conditions, and random arrival of colonizing species (Paine and Levin 1981). Areas of rocky shores in South Africa which were cleared in summer/autumn converged to a single state, with those cleared in winter/spring showing a greater instability which oscillated between three states (Dye 1998). States were characterised by the dominance of species such as *Nodilittorina africana* (Philippi, 1847) and *Tetraclita serrata* Darwin, 1854 or the absence of species such as *Chthamalus dentatus* Krauss, 1848. Dispersal of *Mytilus trossulus* Gould, 1850 and *Mytilus edulis* (L., 1758) after disturbance was shown to increase recovery rate of mussel cover and influence the dynamics of established mussel aggregations (Hunt and Scheibling 1998a). Studies of this nature are usually on a relatively short time scale but it has been shown that recovery of a community, after disturbance, to an initial state occurs over a prolonged period of time. Biological disturbance has been shown to be a significant driving force in determining the return of the community structure back to the original state. This was demonstrated by the use of toxic dispersants to clean up the 'Torrey Canyon' oil-spill in 1967 off the west Cornwall coast which caused a mass mortality of intertidal flora and fauna (see Southward 1978 for a review of the re-colonisation). Re-colonisation started with an initial recruitment of *Enteromorpha* and *Ulva* which was followed by a dense *Fucus* growth establishing a thick canopy. The *Fucus* canopy provided shelter for *Nucella lapillus* (L. 1758) and had a combined effect of decreasing the barnacle abundance. *Patella* species and *Littorina littorea* (L. 1758) began to re-colonise after the first year

which, by the sixth or seventh year, removed the majority of the large algal species. In turn, *Patella* species decreased with the decrease in available food which enabled barnacle species to re-colonise the intertidal with their population peaking in the ninth and tenth years after the oil-spill.

2.1.2 Settlement and recruitment processes of the intertidal

Understanding settlement and recruitment processes in the intertidal is fundamental in order to understand the succession of species re-colonisation. Patterns of settlement of planktonic larval stages of key species can explain much of their distributions along major environmental gradients such as height and wave exposure. Settlement is usually defined as the point when an individual first takes up permanent residence on the substratum, for example in sessile species this is when the planktonic propagule has cemented itself to the surface (Connell 1985), but before permanently recruiting into the population. Factors such as onshore winds, space occupation by metamorphosed barnacles (Knight-Jones and Stevenson 1950; Knight-Jones 1953; Hawkins and Hartnoll 1982), rate of arrival of larvae, active selection of settlement sites (Knight-Jones 1953; Jenkins *et al.* 2000), and species interactions (Jenkins *et al.* 1999c) all affect larval settlement and their potential recruitment to the adult population. Recruitment is not only dependent on factors influencing settlement but also on physical, biotic, and/or chemical factors which have all been shown to influence the distribution of sessile invertebrate recruitment (reviewed by Rodríguez *et al.* 1993) leading to post-settlement mortality. Intertidal temperature fluctuations, latitude (Range and Paula 2001), grazing, background recruitment (Johnson and Hawkins 1998), and the number of competent larvae settling (Rodríguez *et al.* 1993) have been found to affect recruitment intensity and season.

Barnacle recruitment in South Africa was found to be related to the adult population abundance (Dye 1992, 1993). This would depend, to some extent, on space availability and post recruitment mortality with "topping up", the contribution to the annual recruitment by late arriving barnacle cyprids which fill space as it becomes secondarily available due to juvenile mortality (Hawkins and Hartnoll 1982), being of increasing importance in the population dynamics of the community structure. Once species have recruited into the community, temperature effects and food availability were the two main factors influencing high growth rates (Coombs 2002). Low temperature, however, was not found to affect survival and reproduction of adult *Chthamalus* species (Southward and Crisp 1954) although, embryo development rate in the mantle cavity (Hines 1978) and larvae in the plankton (Burrows *et al.* 1999a) were found to be directly influenced by temperature. An increase in the mortality of new recruits of *Chthamalus stellatus* (Poli, 1791) was related to calm weather which increased submersion time (Connell 1961b) and so may have increased predation.

Within a particular area the patch composition and stability seem determined by biological relationships, especially competition (Dayton 1985). In many ecological communities (Connell 1961b; Dayton 1971; Paine and Levin 1981), space is the primary limiting resource and competition at a particular site will invariably eliminate all but a few species. These systems are often characterized by high diversity (Paine and Levin 1981).

The factors discussed above are summarised in Table 2.1 in relation to the scale, regional or local, at which they would have the maximum impact. Abiotic factors are the major factors acting at regional scales with biotic interactions acting at a more local

scale. Food availability was classed within both scales since pelagic food, such as phytoplankton and zooplankton, is widely dispersed within the water column and so would be more dependent on oceanographic conditions. In contrast, food sources for predators and grazers predominate from macro species which have established themselves within the intertidal.

Table 2.1 Factors affecting intertidal recruitment which act at regional and local scales.

Regional scale	Local scale
Abiotic factors	
Climate (temperature, wind speed etc)	Tidal range
Wave exposure	
Oceanographic conditions	
Biotic factors	
Larval supply	Competition (intra- and inter-specific)
Food availability for filter feeders	Food availability for predators and grazers
	Post-settlement mortality

2.1.3 Intertidal barnacle species of western Scotland

Within the Scottish west coast, four species of barnacle commonly occur in the intertidal above mean low water neaps (MLWN); *Chthamalus montagui* Southward, 1976, *C. stellatus*, *Semibalanus balanoides* (L., 1767), and *Elminius modestus* Darwin, 1854.

2.1.3.1 Barnacle species range

Chthamalus stellatus is a Mediterranean-eastern North Atlantic species (Lewis and Powell 1960a) with its centre of distribution in the Mediterranean reaching its northern limit in the Shetland Islands (Connell 1961b) although it was found to be rare or absent in the sheltered lochs along the west coast of Scotland (Southward 1976). These observations were based on findings from North Rona, Skye, and Loch Sween. Although the exact southern limits of *C. montagui* are not known, they can exist in the warmest parts of the Bay of Biscay (Southward 1976) with the northern limit in Orkney. *Semibalanus balanoides*, is a boreoarctic species found on both sides of the Atlantic (Brind'Amour *et al.* 2002) reaching its southern limit, in the eastern Atlantic, in northern Spain (Lewis and Powell 1960a; Connell 1961b). *Elminius modestus*, is an immigrant from Australasia that is thought to have arrived in Europe during World War II and is found to contribute substantially to the barnacle zone in estuarine and sheltered localities in south-east England, the Bristol Channel, and the Irish Sea (Crisp and Southward 1958; Southward 1991) north to Loch Erisort, Isle of Skye (Howson *et al.* 1994) and many other west coast localities, including Lewis and Harris (Burrows M. T., personal communication).

2.1.3.2 Distribution within the intertidal

Within the barnacle zone, species show marked vertical patterns of distribution with *C. montagui* occupying the uppermost of the shore. When this species and *C. stellatus* are both abundant on the shore, the former predominates at mean high water springs (MHWS) and mean high water neaps (MHWN), while the latter is dominant at mid tide

level (MTL) and below (Southward 1976). On Great Cumbrae, Scotland, adults of *C. stellatus* occur between MHWN and MHWS (Connell 1961b) although this species was most probably *C. montagui*. *Semibalanus balanoides* are found from mean low water springs (MLWS) to between MHWN and MHWS (Connell 1961b), constituting the main intertidal barnacle species (Southward 1991) which is found to be more in competition for space on the rock, in SW England, with *C. stellatus* (Southward 1976). *Elminius modestus* can occasionally survive higher on the shore than *S. balanoides* but is usually commonest below MHWN (Southward 1991).

2.1.3.3 Reproduction and settlement of intertidal barnacle species

Both *C. stellatus* and *C. montagui* were found to breed between early May and late September (Burrows *et al.* 1992). Only the settlement of late summer and early autumn led to a successful spat fall for *C. stellatus* at Millport (Barnes 1956). *Chthamalus stellatus* produce two broods annually between May and September (Crisp 1950; Powell 1954; Barnes 1972; Achituv and Barnes 1976). The length of the breeding season is usually defined by temperature (Hines 1978) with the onset of breeding in France of *C. stellatus* occurring in April when mean air and seawater temperatures were 11 to 12°C with a maximum air temperature of about 14°C (Barnes 1992). These southern species were found to breed continuously over a prolonged season (Barnes 1956 for *C. stellatus*; Patel and Crisp 1960; Burrows *et al.* 1992 for *C. stellatus* and *C. montagui*). Breeding time is also dependent on shore height, as well as brood size and number which has also been shown to vary with year class and location (Burrows *et al.* 1992; O'Riordan *et al.* 1992). Earlier breeding was found in *C. stellatus* at lower tidal levels with the reverse found in *S. balanoides* (Barnes 1989).

Adult *S. balanoides* produce one brood per year in autumn (Patel and Crisp 1960) of 400 to 8 000 eggs which hatch internally (Barnes and Powell 1968). The larvae are released into the plankton between March and April (Crisp 1964) and, once settled onto a substrate, have an average metamorphosis time of 1.5 days (Jenkins *et al.* 2000) with juveniles maturing at one to two years (Arnold 1977).

Elminius modestus is capable of breeding throughout the year (Lawson *et al.* 2004). At the northernmost limits of its distribution it has a more seasonal breeding pattern (Barnes 1989) with undeveloped ovaries found during winter months in Cork harbour, Ireland (O'Riordan and Murphy 2000) and settlement occurring between May and October (Crisp 1958; Jones 1961; Lawson *et al.* 2004).

2.1.4 Aims and hypotheses

The primary aim of this chapter was to determine whether community structure and species composition and abundance varied between the two regions with the Clyde system dominated by large filter feeders and the west coast by macroalgae. This in turn led to the secondary aim testing that greater pelagic primary production in the Clyde system promotes success in larval development and growth of intertidal barnacle species.

These aims were addressed by comparing recruitment of the major intertidal fauna and flora in two contrasting regions of pelagic primary productivity, the Clyde system and the west coast, and investigating densities and growth rates of intertidal barnacle species with regard to the following null hypotheses:

- Population turnover does not differ between regions.
- Intertidal barnacle density and growth rates are not influenced by large scale regional differences.

The experiment was designed to determine the impact which disturbance (section 2.1.1) would have on the settlement and recruitment (section 2.1.2) of intertidal flora and fauna between two regions of differing pelagic primary productivity by using time-series photographic analysis. A similar technique, although at a smaller scale of area, was used to test the influence of large scale regional differences on intertidal barnacle species (section 2.1.3) by measuring their growth rates with the aid of an image analysis program.

From the literature discussed within this section and those discussed in Chapter 1, predictions as to the effects of differing pelagic primary productivity could be made. Filter feeders would be expected to be found in large quantities growing to a large size in the Clyde due the increased availability of food found within this area. A large embayment, such as the Clyde, would be expected to have an increased larval supply leading to an increased productivity of filter feeders. It would be predicted that intertidal communities within the Clyde would be more stable than those on the more open west coast which would be affected by loss of larvae due to increased offshore advection. An increased macroalgal cover would be expected to dominate the west coast as found in similar studies examining variation in community structure between upwelling and downwelling regions of New Zealand (Menge *et al.* 1999; Menge *et al.* 2002), South Africa (Menge 1995; Bustamante and Branch 1996b, 1996a; McQuaid and Lindsay 2000), Chile (Wieters *et al.* 2003; Nielsen and Navarrete 2004; Lagos *et al.* 2005), California (Dayton *et al.* 1999), and Oregon (Menge *et al.* 1997b; Menge *et al.* 2002).

Abundances of flora and fauna found within each area of study is important when comparing results from different experiments. A working knowledge of species composition and structure over varying spatial scales will aid in predicting future expectations of intertidal community structure. These data, combined with data from other chapters, will help in determining whether the area is driven by bottom-up or top-down effects.

2.2 Materials and Methods

2.2.1 Preliminary surveys of regional and local variation in community structure

In October 2003 fourteen sites (Figure 2.1) in five lochs (Appendix 2.1) were visited to estimate the abundance of intertidal biota using categorical abundance scales, a modified SACFOR scaling system (Appendix 2.2) as originally described by Crisp and Southward (1958). Thirty minutes were spent at each site looking for key species (Appendix 2.3). The shore profile of each site was taken from the water's edge to the top of the littoral fringe by recording distance up the shore at every 0.5 m height interval. The shore profile was used as a mid-point in defining the boundaries of the search area which extended 25 m horizontally on either side of the mid-point and vertically from the waters edge to the top of the littoral fringe. All sites consisted of bedrock or large, static, boulders with easy road access to ensure a maximum number of sites visited per day. The location of each site was recorded using a Garmin GPS 76 in order to facilitate in the re-location of sites.

2.2.2 Design and establishment of colonisation and monitoring areas

Four loch systems, two on the west coast of Scotland (Loch Melfort and Loch Caolisport) and two in the Clyde system (Loch Long and Loch Fyne), were chosen as sampling areas. Two west facing sampling sites were located in each loch, one at the mouth and the other half way up the loch (termed inner) (Figure 2.1). Each site consisted of bedrock or large, static, boulders. Sites were chosen to ensure maximum similarity in all aspects apart from region, thereby reducing the effects of local influences such as wave exposure, circulation, salinity, sunlight, and profile (Table 2.2).

Due to the large distances between sites and lochs, easy vehicular access was deemed to be important in order to maximise time spent at each site. An initial shore profile was calculated from the water's edge up the shore to the top of the littoral fringe by recording the distance from the water's edge at every 0.5 m increment in elevation. Increments of elevation were calculated using two bamboo canes and line of sight of two pre-marked cane heights with the horizon. The cane situated closer to the waters edge was pre-marked at a height of 1.5 m and the cane further up the shore at 1.0 m. The cane furthest from the waters edge was moved along the transect until both marks were visually aligned with the horizon. The distance along the transect was noted and the cane closest to the waters edge was then placed at this location. The process was repeated to the top of the littoral fringe. A rule of twelfths design was then used to calculate the height up the shore of mean high water neaps (MHWN) and mean low water neaps (MLWN) dependent on the time of arrival at each site. Two shore heights, upper and lower, were established 1.0 m below MHWN and MLWN, respectively. Sixteen permanent quadrats, eight 30x30 cm and eight 5x5 cm, were randomly located at each height. Three 7 mm diameter holes were drilled, about 8mm deep, with a 24V cordless hammer drill for each quadrat for locating the legs of two purpose built tripod camera frames. Each hole was marked with red paint (QD90 machinery and metal paint, Blackfriar®) for easy future location. All quadrats were photographed, using a coin as a scale, with a Ricoh Caplio RR30 digital camera (2048 normal picture quality) mounted on one of the two frames (Figure 2.2). Four 30x30 cm quadrats and four 5x5 cm quadrats were cleared of all fauna and flora using paint scrapers and wire brushes. All cleared areas were re-photographed. Sketches of the area were drawn as well as photographs taken to enable easy re-location of quadrats. The location of each site was recorded using a Garmin GPS 76 in order to facilitate in the re-location of sites.

Sampling started in March 2003 with each site visited, where possible, every three months. On each visit, quadrats were located, marks re-painted, and areas photographed as described previously. Sampling was completed in June 2005.

Table 2.2 Factors which could potentially confound comparisons and precautions which were taken in order to minimise the bias of each factor at a scale of inner and mouth sites.

Factor	Precaution
Wave exposure	All sites were west facing with inner and mouth locations in order to enhance similarity in wave fetch and aspect at each site. Sites were chosen which consisted of similar biological characteristics so as to minimise the effect of exposure (see Ballantine 1961).
Circulation	Potential difference between inner and mouth sites. Inner sites may have reduced circulation, compared to sites at the mouth, due to flushing times of lochs which may increase water flow at mouth sites. This effect would be reduced by positioning the inner site half way up each loch system.
Salinity	Care was taken not to situate sites close to freshwater inflows such as rivers and streams and all lochs were chosen with similar freshwater input relative to their size.
Sunlight	All shores were west facing to ensure similarity of light intensity with regard to the position of the sun.
Profile	Shore profiles were taken at each site from the waters edge to the top of the littoral fringe.

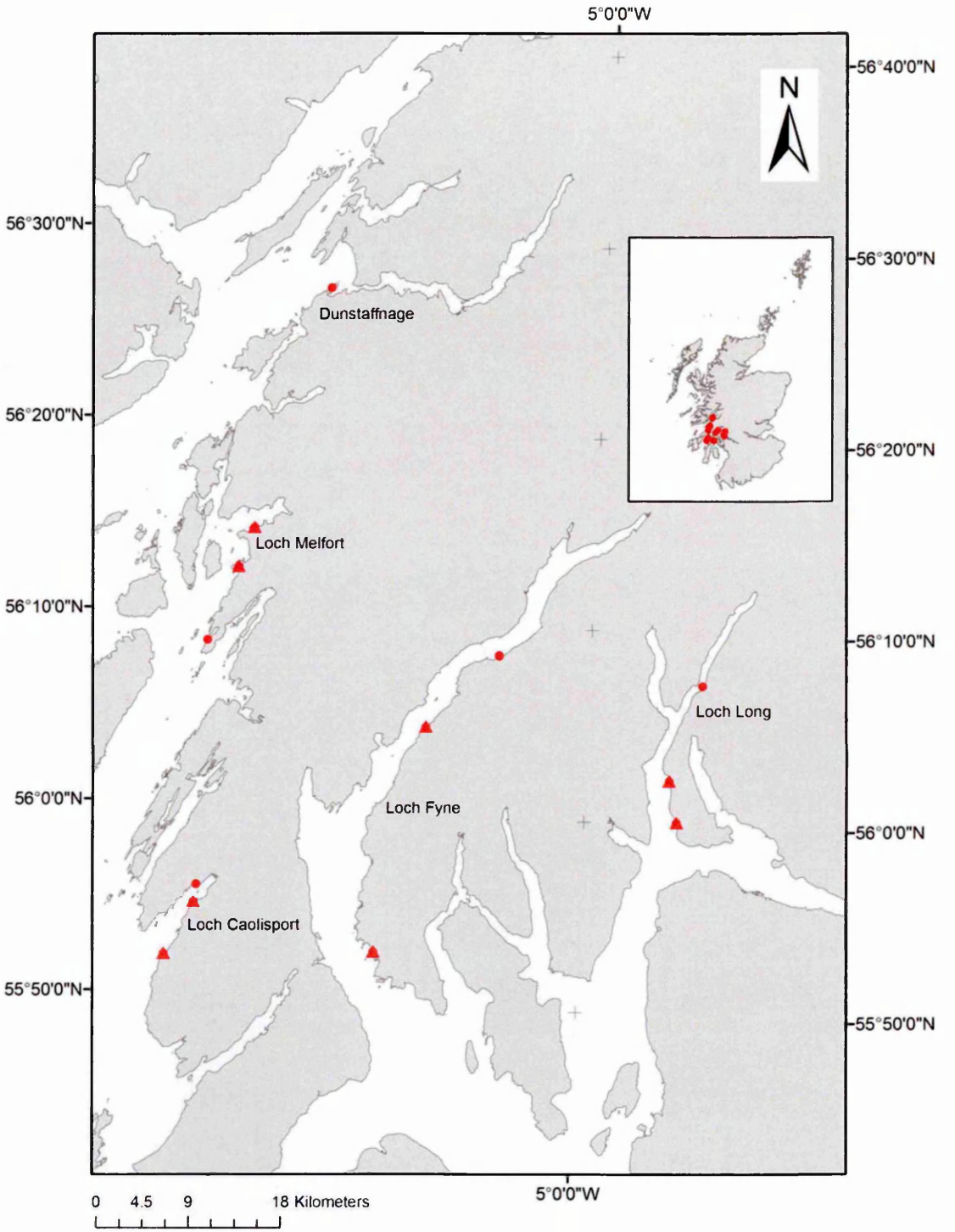


Figure 2.1 Permanent monitoring sites (triangles) with additional sites which were visited to estimate species abundance (circles) are shown. The map insert shows the location of the sites within Scotland.

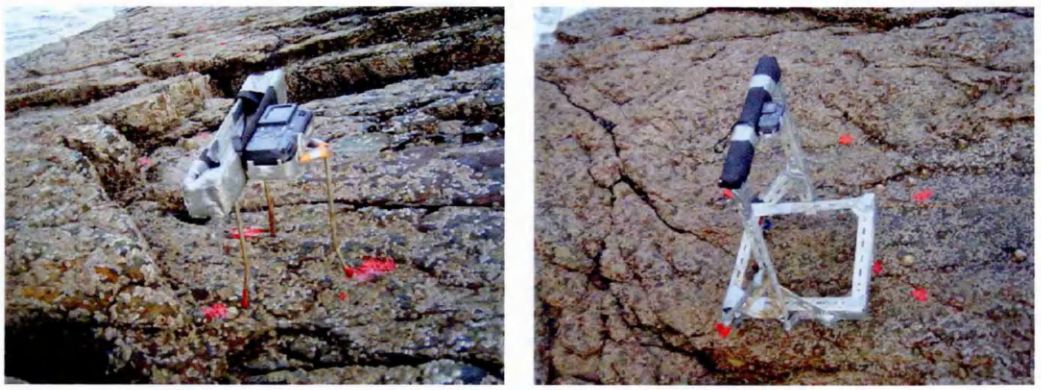


Figure 2.2 Photographs of the custom-built frames with the camera attached. Each frame was used to enable repeated recording of quadrats of two sizes (5x5 cm on the left and 30x30 cm on the right).

2.2.3 Image analyses prior to estimation of abundances and length measurements

Although custom built frames were used for all photographs throughout the study period, it was not possible to take exactly the same image on every occasion due to small variation in depths of the holes locating the tripod legs and growth and colonization of the area in and around each hole. For this reason, images within each time series were rotated to ensure each image showed exactly the same area. A PC program was used to display both the original image and the image to be rotated and, by flipping between the two images, to identify reference points in each image. Using coordinates of these points the angle of rotation was calculated and this angle used to generate a new, rotated image. This process was carried out throughout the time series for all images in both quadrat sizes.

2.2.4 Determination of the abundance of major species

Species abundance and counts within the 30x30 cm quadrats (see section 2.2.2) were determined, specifically the abundances of barnacle species, macroalgae, and *M. edulis* as well as counts of *Patella vulgata* (L., 1758), *N. lapillus*, and *Littorina* species, specifically *L. littorea*, *Littorina obtusata* (L., 1758), *Littorina mariae* Sacchi & Rastelli 1966, and *Littorina saxatilis* (Olivi, 1792). By defining the length of the scale object in the rotated image, a PC program was used to overlay a grid, with each grid cell being 3 cm by 3 cm on each image. A 900 cm^2 area was defined from the top left of each image with a visual abundance estimate of all sessile flora and fauna within each quadrat taken and all mobile animals were counted.

2.2.5 Density, length, and growth of intertidal barnacle species using image analysis

All 5x5 cm quadrat images were analysed in the same way as the 30x30 cm quadrats but with the overlaid grid having 1 cm^2 cells. A 9 cm^2 area was defined in the top right of each picture and all barnacles within this area were identified. After identification, each species was measured by marking the apex of the tergum followed by the base of the scutum (Figure 2.3 and Figure 2.4). All lengths were recorded in a comma-separated-value file which was imported to Excel for further analysis. The increase in size of the whole animal would be better measured by volume changes, but since the shape does not change greatly with age, the length may be conveniently used and can be more readily compared with other works (Barnes and Powell 1968). Barnacle density and average lengths of the populations were estimated throughout the time series. The increase in size of each species was determined as a population growth in relation to settlement time. The defined 9 cm^2 area of each image enabled the same area of barnacles to be measured over time with each new settlement analysed separately.

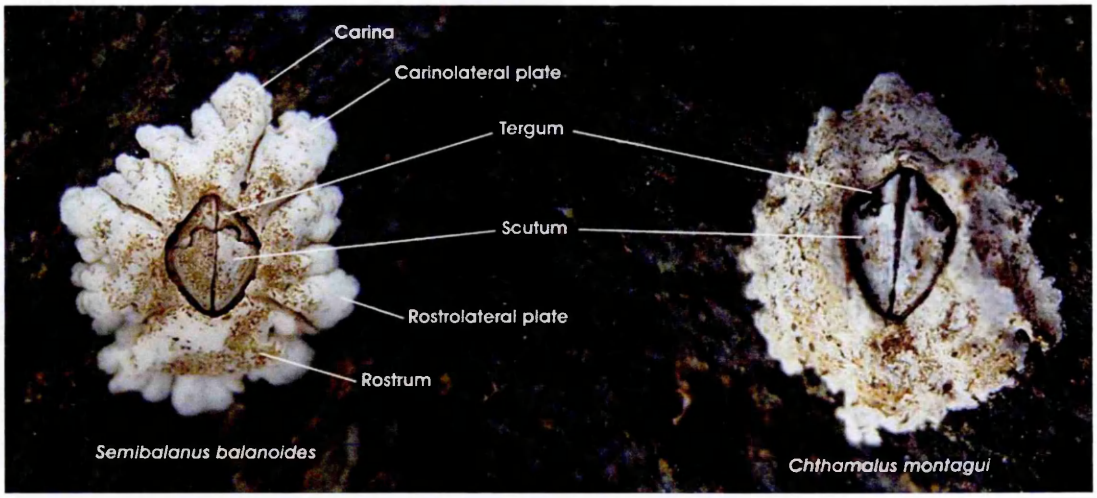


Figure 2.3. Two barnacle species, *S. balanoides* (left) and *C. montagui* (right) are shown. Shell plates of *S. balanoides* and opercular plates of both species are labelled.

Figure 2.4. An example of the program used to measure barnacle opercular lengths. Each colour represents a different species namely, *S. balanoides* (dark blue), *C. montagui* (light blue), and *C. stellatus* (yellow). The coin was used as a scale which is 18.0 mm in diameter with the blue square denoting the study area.

2.3 Results

2.3.1 Preliminary surveys of regional and local variation in community structure

Abundance estimates of flora and fauna were analysed using the PRIMER software package (Plymouth Routines in Multivariate Ecological Research, version 6.1.5, Clarke and Gorley 2006). The data were not transformed as all scales used to calculate abundances followed a log distribution (see Appendix 2.2). A cluster analysis dendrogram and a non-metric multi-dimensional scaling (MDS) ordination based on Bray-Curtis similarities were constructed (Figure 2.5 and Figure 2.6, respectively). Similarities of 70% and 77% were overlaid on the MDS showing two distinct groups at the 70% level. All west coast sites were grouped together as were Clyde sites with the exception of the mouth site at Loch Fyne which was grouped on its own. The stress, a measure of how good the representation of the MDS fits the data, of the 2D MDS was 0.14 which is considered to be slightly high but it should be noted that the stress of the 3D equivalent was 0.08 which shows a good representation of the data. This decrease in stress with an increase in dimensionality is to be expected.

Table 2.3 Species contributing to the dissimilarities between the west coast of Scotland and the Clyde system from a one-way SIMPER analysis. Mean abundances correspond with SACFOR scaling system described in Appendix 2.2.

Species	Mean abundance		Contribution (%)	Cumulative (%)
	West coast	Clyde		
Mytilus edulis	2.13	5.33	4.92	4.92
Littorina obtusata	1.75	3.83	3.93	8.85
Pomatoceros triqueter	1.00	3.83	3.89	12.74
Ascophyllum nodosum	4.13	4.17	3.86	16.60
Lichina pygmaea	4.00	2.00	3.78	20.38
Laminaria digitata	3.88	1.83	3.76	24.14
Littorina littorea	2.88	4.83	3.59	27.73
Enteromorpha spp.	1.75	3.83	3.57	31.30
Chthamalus montagui	4.13	2.17	3.51	34.81
Spirorbis spirorbis (*borealis*)	1.00	3.50	3.35	38.16
Cladophora rupestris	1.88	4.17	3.32	41.48
Fucus vesiculosus	5.75	3.50	3.29	44.77
Coralline crusts (high pools)	3.13	1.83	3.20	47.97
Polysiphonia lanosa	2.38	3.67	3.19	51.16

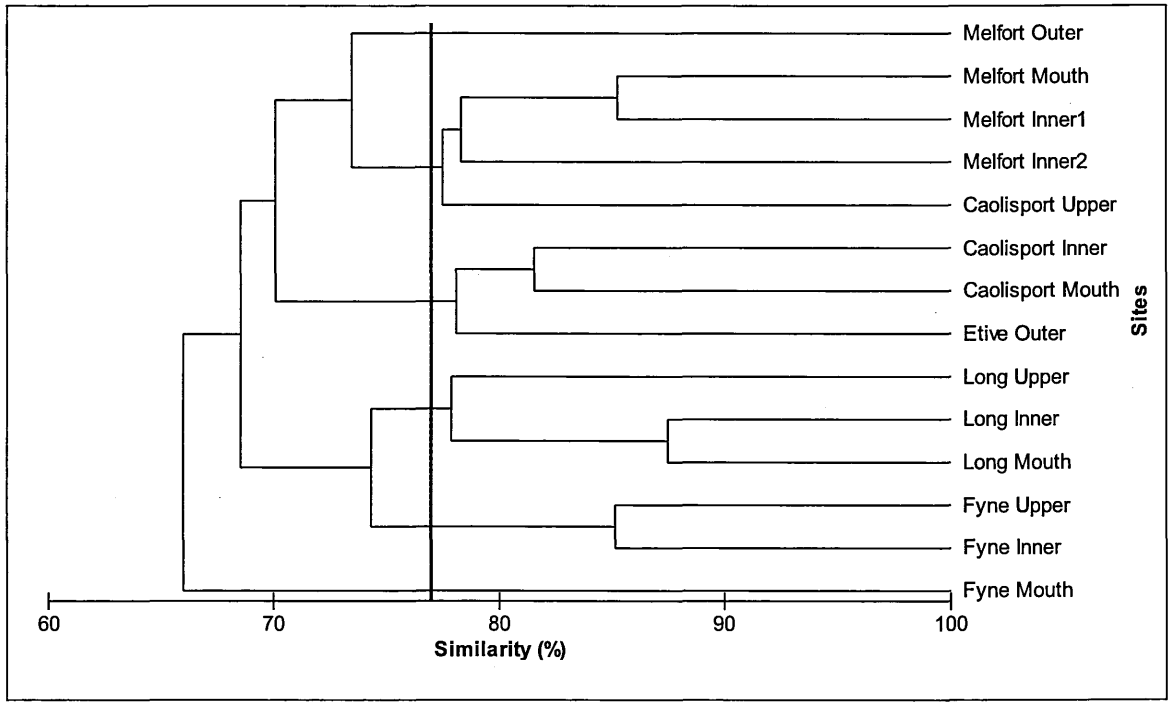


Figure 2.5 A dendrogram based on Bray-Curtis similarities of the 14 sites within five loch systems (Appendix 2.1). The solid vertical line represents a similarity of 77%.

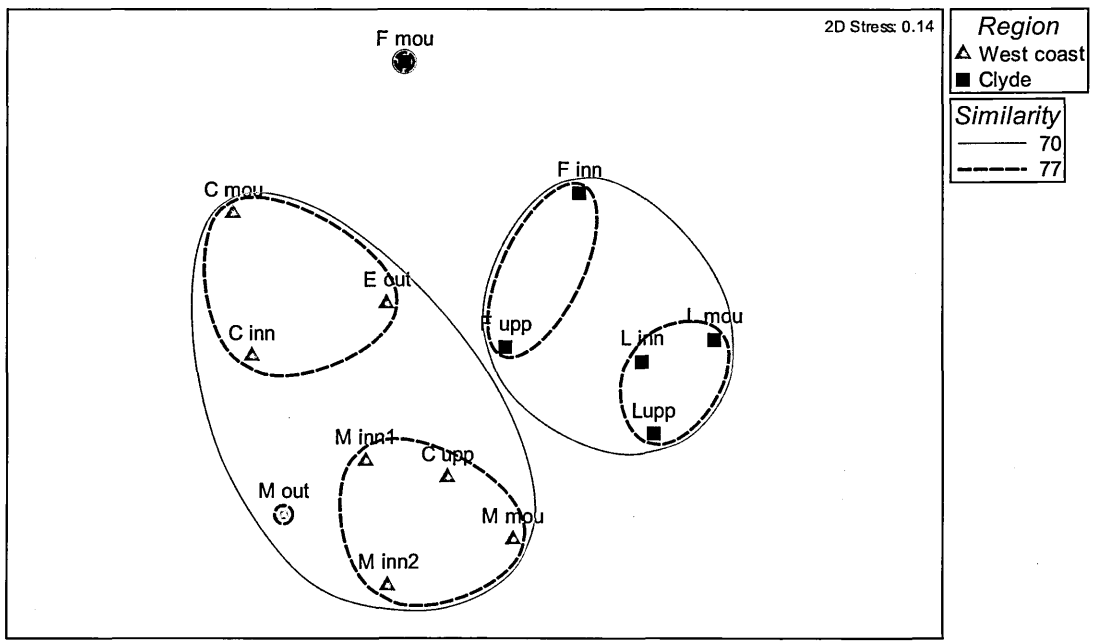


Figure 2.6 Non-metric multi-dimensional scaling (MDS) ordination based on Bray-Curtis similarities from 14 sites in five different loch systems (see Appendix 2.1 for site details). Similarities of 70% (solid line) and 77% (broken line) are shown.

Rocky shore communities on the west coast of Scotland were significantly different from those in the Clyde system (one-way ANOSIM, R = 0.532, P<0.001) which is apparent at the 70% similarity level (Figure 2.5 and Figure 2.6). In order to determine which species contributed to the dissimilarity between regions, a one-way SIMPER analysis was carried out (Table 2.3). The top five species accounted for 21% of the cumulative contribution (Table 2.3) with *M. edulis* found to have the greatest dissimilarity between regions. *Mytilus edulis*, *L. obtusata*, and *Pomatoceros triqueter* (L., 1758) were all found to have mean abundances greater in the Clyde. *Lichina pygmaea* (Lightfoot) Agardh, 1821 was the only species, out of the top five, which was found to have a greater mean abundance on the west coast while *Ascophyllum nodosum* (L.) Le Jolis, 1863 was found to have a similar mean abundance within both regions (Table 2.3).

2.3.2 Long term variation in abundance of major intertidal species

Due to the nature of the experimental design with replicates occurring at the same area at each sampling period a repeated measures multivariate ANOVA approach was initially considered. Although a MANOVA would be an ideal test to examine variation in species abundance over time, the complex nested experimental design with lochs (a random factor) nested within region (fixed factor), precluded the use of MANOVA. For this reason, it was decided to use a combination of a summary statistics approach to repeated measurements analysis and nested ANOVAs. Summary statistics were calculated from averages of each species within each quadrat over time taking into account missing values. The subsequent analysis of the data was then treated as a conventional nested ANOVA. Since it was necessary to discard some data when calculating the summary statistics, nested ANOVAs were run on four time periods

(August 2003, March 2004, September 2004, and March 2005). These times corresponded with periods of low (March 2004 and 2005) and high (August 2003 and September 2004) cover.

Throughout the study period, seven major animal taxa (barnacle species, *M. edulis*, macroalgae, *P. vulgata*, *N. lapillus*, *L. littorea*, and other *Littorina* species) were identified for analysis. Due to the low abundances of *Pelvetia canaliculata* (L.) Decaisne & Thuret, 1845, *A. nodosum*, *Fucus spiralis* L., 1753, *Fucus vesiculosus* L., 1753, and *Fucus serratus* L., 1753 within the sampling quadrats, these species were combined into one group, macroalgae. A total of 21 different species were observed within the 30x30 cm quadrats throughout the study area. Species recorded at every location included; unidentified barnacle species, *M. edulis*, *A. nodosum*, *P. canaliculata*, *F. spiralis*, *F. vesiculosus*, *F. serratus*, *P. vulgata*, *N. lapillus*, *Gibbula umbilicalis* (da Costa, 1778), *L. littorea* and other *Littorina* species. Nine additional species were recorded but were not found to be present at every site (Table 2.4).

Table 2.4 Presence (denoted by a ✓) of the nine species which were not observed at every site within the 30x30 cm quadrats throughout the study area.

	Osmundea pinnatifida	*Lithophyllum* spp.	*Lichina pygmaea*	*Enteromorpha linza*	*Cladophora rupestris*	*Palmaria palmata*	*Ulva lactuca*	*Chondrus crispus*	*Asterias rubens*
Fyne inner upper									
Fyne inner lower									✓
Fyne mouth upper									
Fyne mouth lower									
Long inner upper	✓								
Long inner lower	✓			✓					
Long mouth upper	✓				✓				
Long mouth lower					✓	✓	✓		✓
Caolisport inner upper			✓						
Caolisport inner lower	✓	✓							
Caolisport mouth upper			✓				✓		
Caolisport mouth lower	✓	✓							
Melfort inner upper									
Melfort mouth upper			✓						
Melfort mouth lower		✓	✓					✓	✓

2.3.2.1 Barnacle cover from 30x30 cm quadrats

Barnacle cover fluctuated throughout the study period at all sites (Figure 2.7, Figure 2.8, and Figure 2.9). Peaks in barnacle cover occurred during August 2003 and September 2004 with troughs in March 2004 and 2005. The general trend, although not significant (nested ANOVA, Summary statistics, $F_{1,113} = 1.98$, $P = 0.288$, Appendix 2.4), was that the Clyde had a higher barnacle cover with Loch Fyne having the largest average cover throughout the study period of 64.4% (range 17.5 to 91.3%). Slightly less barnacle cover was seen in Lochs Long (mean = 47.1%, range 0 to 86%), Caolisport (mean = 40.8%, range 1 to 82.5%), and Melfort (mean = 44.6%, range 4.2 to 95%). However, a regional difference was seen in September 2004 (Table 2.5, Appendix 2.6) with more barnacles found in the Clyde system although this difference was not found in August 2003 (nested ANOVA, $F_{1,57} = 0.46$, $P = 0.667$, Appendix 2.5), March 2004 (nested ANOVA, $F_{1,57} = 0.46$, $P = 0.667$, Appendix 2.5), or March 2005 (nested ANOVA, $F_{1,74} = 1.58$, $P = 0.315$, Appendix 2.6). Upper shores at Lochs Long, Caolisport, and Melfort had a significantly greater amount of barnacle cover compared to the lower with the opposite found in Loch Fyne (nested ANOVA; Summary statistics, Appendix 2.4; August 2003, Appendix 2.5; March 2005, Appendix 2.6; Table 2.5). Barnacles were found to be more abundant at cleared areas of lower shore heights and un-cleared areas from upper heights (nested ANOVA; summary statistics, Appendix 2.4; August 2003, Appendix 2.5; March 2005, Appendix 2.6; Table 2.5) with only Loch Long showing a greater barnacle cover at cleared areas compared with non-cleared areas (nested ANOVA, summary statistics, Table 2.5 and Appendix 2.4). Differences in barnacle cover were seen between inner and mouth positions within lochs with inner positions found to have a greater barnacle cover in Lochs Long, Fyne, and Caolisport in March 2005 (Table 2.5 and Appendix 2.6).

Table 2.5 Summary of the significant nested ANOVA interactions for barnacle cover. Significant results (0.05≥*P>0.01; 0.01≥**P≥0.001; ***P<0.001) are shown against the F ratio. Interactions significant at P≤0.01 are shown in bold. (++ denominator of the F test is zero)

Interaction	Summary	August 2003	March 2004	September 2004	March 2005
Region	1.98	0.93	0.46	27.51**	1.58
Region×Height	0.14	0.22	++	4.18*	0.27
Position×Cleared	1.99	0.76	0.25	0.63	6.22*
Height×Cleared	5.59*	11.10**	3.79	2.93	5.00*
Position×Loch(Region)	2.70	1.05	0.31	1.00	8.64***
Height×Loch(Region)	4.48*	6.45**	<0.01		5.84**
Cleared×Loch(Region)	4.03*	1.89	1.19	2.83	1.38
Region×Position×Cleared	0.65	1.18	1.16	4.96*	1.64
Region×Height×Cleared	0.70	2.66	0.13	1.68	4.71*

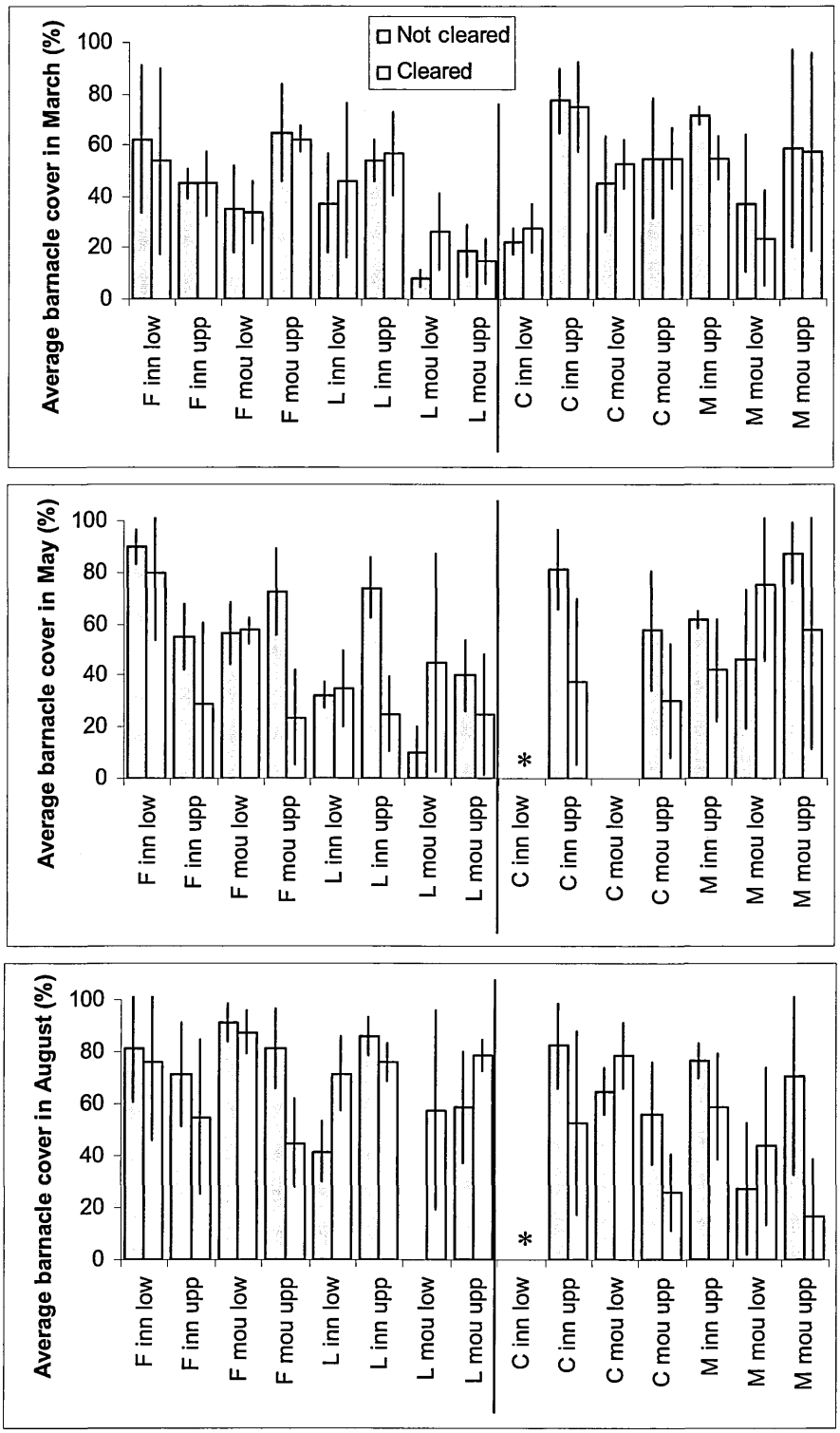


Figure 2.7 Average barnacle cover for March, May, and August 2003. Lower (low) and upper (upp) shores of the inner (inn) and mouth (mou) of each of Lochs Fyne (F), Long (L), Caolisport (C), and Melfort (M) are shown with corresponding 95% CI. Cleared areas in March were prior to clearing. * denotes sites which were not sampled.

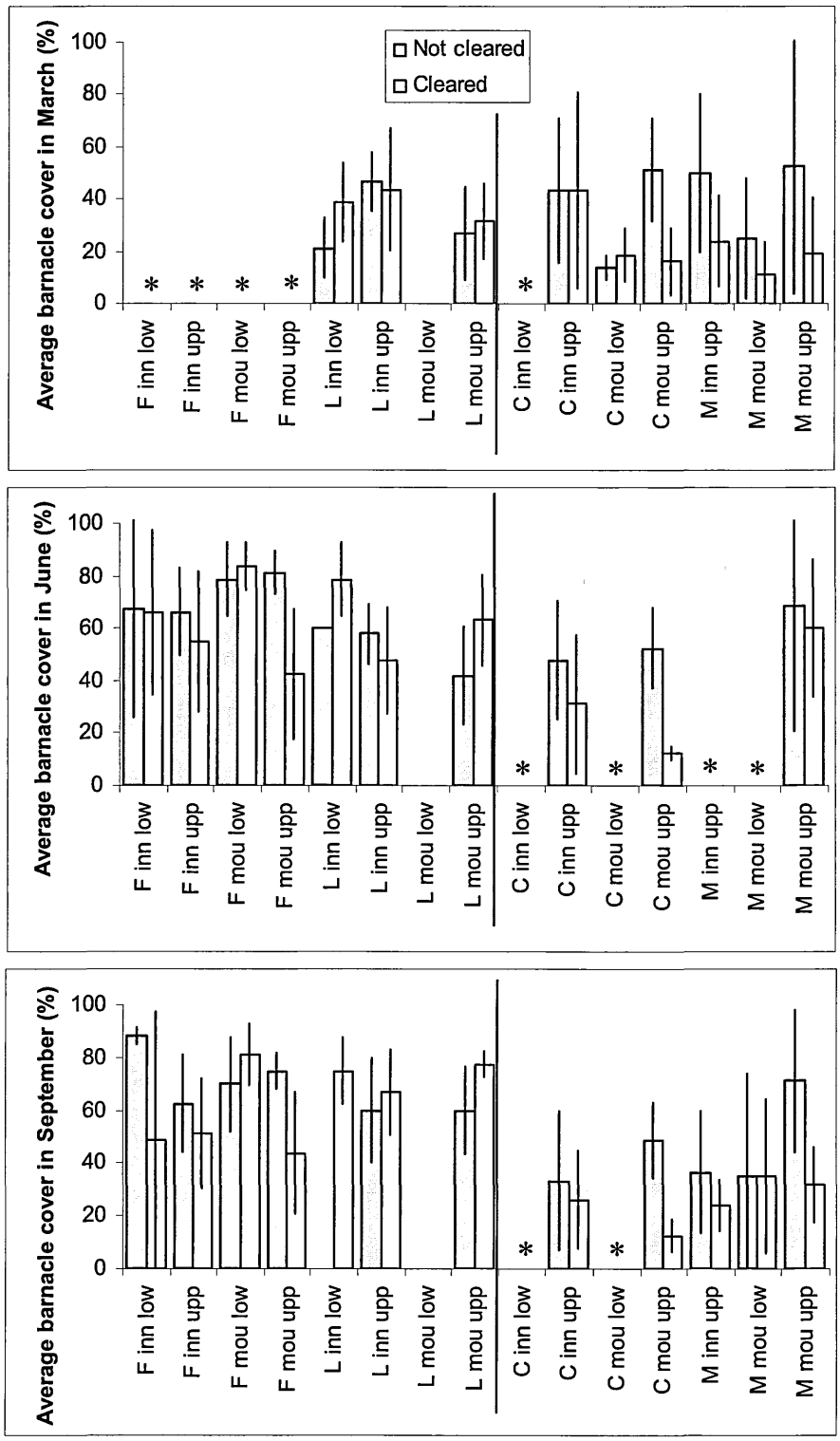


Figure 2.8 Average barnacle cover for March, June, and September 2004 are shown for all sites in Lochs Fyne, Long, Caolisport, and Melfort. Corresponding 95% confidence intervals are shown. * denotes sites which were not sampled.

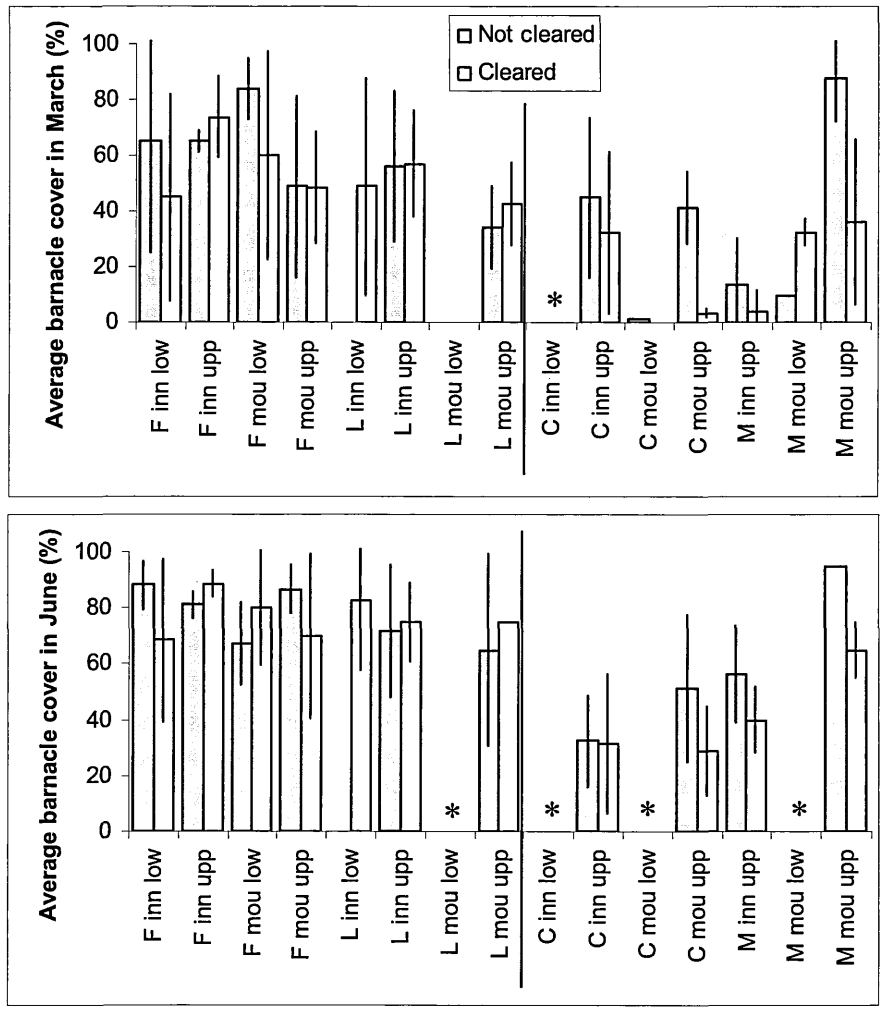


Figure 2.9 Average barnacle cover for March and June 2005 are shown for all sites in Lochs Fyne, Long, Caolisport, and Melfort. Corresponding 95% confidence intervals are shown. * denotes sites which were not sampled.

2.3.2.2 *Mytilus edulis* cover from 30x30 cm quadrats

Mytilus edulis were found to be scarce throughout the majority of the study area with none found within quadrats in Loch Caolisport and very few found in Loch Fyne (mean = 0.004 m^{-2}, maximum = 0.3 m^{-2}) and Loch Melfort (mean = 0.03 m^{-2}, maximum = 0.3 m^{-2}, Figure 2.10). Loch Long had the greatest *M. edulis* cover with a mean of 17.9 m^{-2} (maximum = 100 m^{-2}). The preliminary investigation found this species to be the thirteenth most abundant throughout the study area with the greatest contribution to the dissimilarities found between the two regions (see section 2.3.1). The greatest average mussel cover was found at the mouth of Loch Long on the lower shore in areas which were not cleared (Figure 2.10). Fewer areas were found over time at lower shores of Loch Long and by March 2005 all areas at both lower shores of the inner and mouth sites were completely covered with mussels.

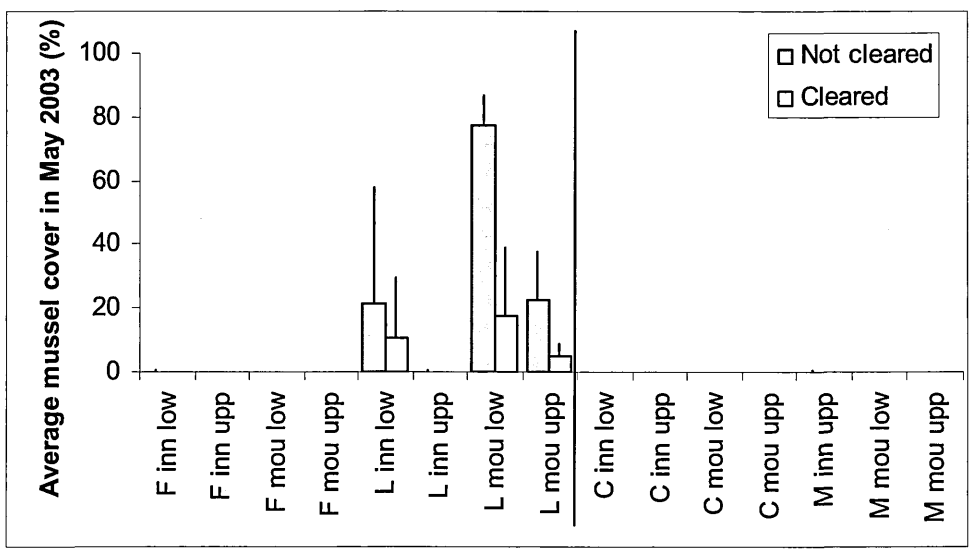


Figure 2.10 Average *Mytilus edulis* cover with corresponding 95% confidence intervals during May 2003.

2.3.2.3 Macroalgal cover from 30x30 cm quadrats

The west coast had a significantly greater macroalgae cover than the Clyde system (nested ANOVA; summary statistics, Appendix 2.7; September 2004, Appendix 2.9; Table 2.6) with an average cover throughout the study period of 19.3% for Loch Caolisport (maximum = 62.5%) and 19.6% for Loch Melfort (maximum = 78.3%). Lochs Fyne (mean = 3.8%, maximum = 21.3%) and Long (mean = 3.7%, maximum = 16.7%) had a considerably lower macroalgae cover (Figure 2.11). No macroalgae were found at the mouth of Loch Fyne, at either the upper or lower shore heights, or on the upper shores of the inner site of Loch Melfort. It should be noted however that the inner site of Loch Melfort was dominated by dense concentrations of *A. nodosum* from MTL down the shore. Due to this, no quadrats were established at the lower shore level of this inner site. A significantly greater cover of macroalgae was found at the mouth of Lochs Long and Melfort and at the inner sites of Lochs Fyne and Caolisport (nested ANOVA, summary statistics, Table 2.6 and Appendix 2.7). Monthly analysis showed the inner sites of Lochs Fyne, Long, and Caolisport to have a higher percent cover of macroalgae with Loch Melfort having a higher cover at the mouth of the loch (nested ANOVA; August 2003 and March 2004, Appendix 2.8; September 2004 and March 2005, Appendix 2.9; Table 2.6). All lochs, apart from Loch Melfort, had significantly more cover of macroalgae at quadrats which were not cleared (nested ANOVA, summary statistics, Table 2.6 and Appendix 2.7).

Table 2.6 Summary of the significant nested ANOVA interactions for macroalgal cover. Significant results (0.05≥*P>0.01; 0.01≥**P≥0.001; ***P<0.001) are shown against the F ratio. Interactions significant at P≤0.01 are shown in bold.

	Summary	**August 2003**	**March 2004**	**September 2004**	**March 2005**
Region	21.48*	3.59	42.23	8.35*	2.32
Cleared	0.06	0.02	0.05	12.97*	1.93
Height×Cleared	1.70	0.01	1.80	11.17**	1.49
Position×Loch(Region)	20.59***	7.35**	15.25***	19.48***	12.95***
Cleared×Loch(Region)	3.14*	1.86	4.78*	1.92**	1.89
Region×Height×Cleared	0.66	0.01	0.65	10.34**	3.00

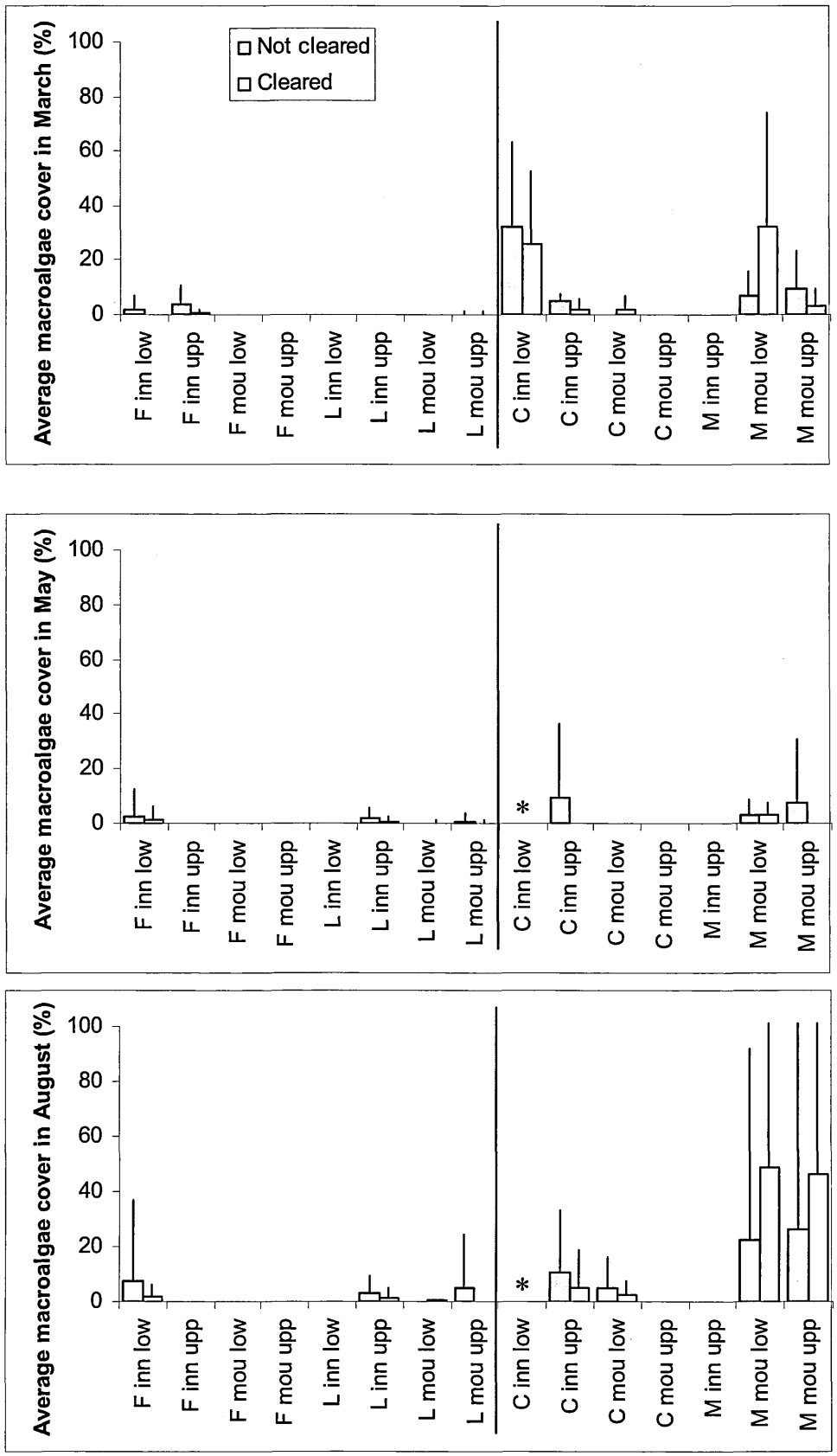


Figure 2.11 Average macroalgae cover with corresponding 95% confidence intervals for three months during 2003. * denotes sites which were not sampled.

2.3.2.4 *Patella vulgata* density from 30x30 cm quadrats

Patella vulgata were found throughout the study area (Figure 2.12). The lowest mean density was found at Loch Caolisport (mean = 3.5 m^{-2}, maximum = 15.3 m^{-2}) and Long (mean = 7.6 m^{-2}, maximum = 66.7 m^{-2}) and the highest at Loch Fyne (mean = 12.4 m^{-2}, range 2.1 to 42.0 m^{-2}) and Melfort (mean = 12.3 m^{-2}, maximum = 88.9 m^{-2}). Height up the shore was the main factor found to be contributing to differences in limpet density with greater densities found at the lower shore within each loch (Table 2.7 and Appendix 2.10) and within loch positions (Table 2.7 and Appendix 2.12). Monthly analysis supported the findings of the summary statistics with height found to be a significant factor contributing to density differences in *P. vulgata*. This was seen for the factor Loch within Region which showed significantly different density levels during August 2003 (Table 2.7 and Appendix 2.11), March 2005 (Table 2.7 and Appendix 2.12), and March 2004 (Table 2.7 and Appendix 2.11), although the latter was not significant at $P<0.05$. Inner positions had a greater density of *P. vulgata* compared to those at the mouth (nested ANOVA; summary statistics, Appendix 2.10; August 2003, Appendix 2.11; Table 2.7). Densities were found to be significantly different when examining the interaction of Position by Loch within Region for September 2004 and March 2005 (see Table 2.7 and Appendix 2.12) although the interpretation was not as clear with only Lochs Fyne and Melfort having greater densities at inner sites in September 2004 but by March 2005 only Loch Fyne had a greater density at the inner site. Colonisation of cleared areas by *P. vulgata* was not seen one year after clearing areas of fauna and flora in March 2004 (Table 2.7 and Appendix 2.11). This pattern was noted in March 2005 although Loch Long showed a greater density of *P. vulgata* at cleared areas with Lochs Fyne, Caolisport, and Melfort having a greater density at non-cleared areas (Table 2.7 and Appendix 2.12).

Table 2.7 Summary of the significant nested ANOVA interactions for *P. vulgata* densities. Significant results (0.05≥*P>0.01; 0.01≥**P≥0.001; ***P<0.001) are shown against the F ratio. Interactions significant at P≤0.01 are shown in bold.

	Summary	**August 2003**	**March 2004**	**September 2004**	**March 2005**
Position	12.42	9.77*	0.79	0.61	4.99
Height	8.52	5.21	2.74	8.35**	3.73
Cleared	2.75	15.85**	1.31	1.28	0.40
Region×Cleared	0.50	0.06	0.17	10.84**	0.10
Position×Height	4.21*	0.57			13.13**
Position×Loch(Region)	1.45	0.53	1.84	5.43**	4.35*
Height×Loch(Region)	3.01	3.51*	3.72		4.94**
Cleared×Loch(Region)	1.79	0.50	5.74*	0.51	5.25**
Region×Height×Cleared	0.01	0.34	1.56	4.58*	0.06

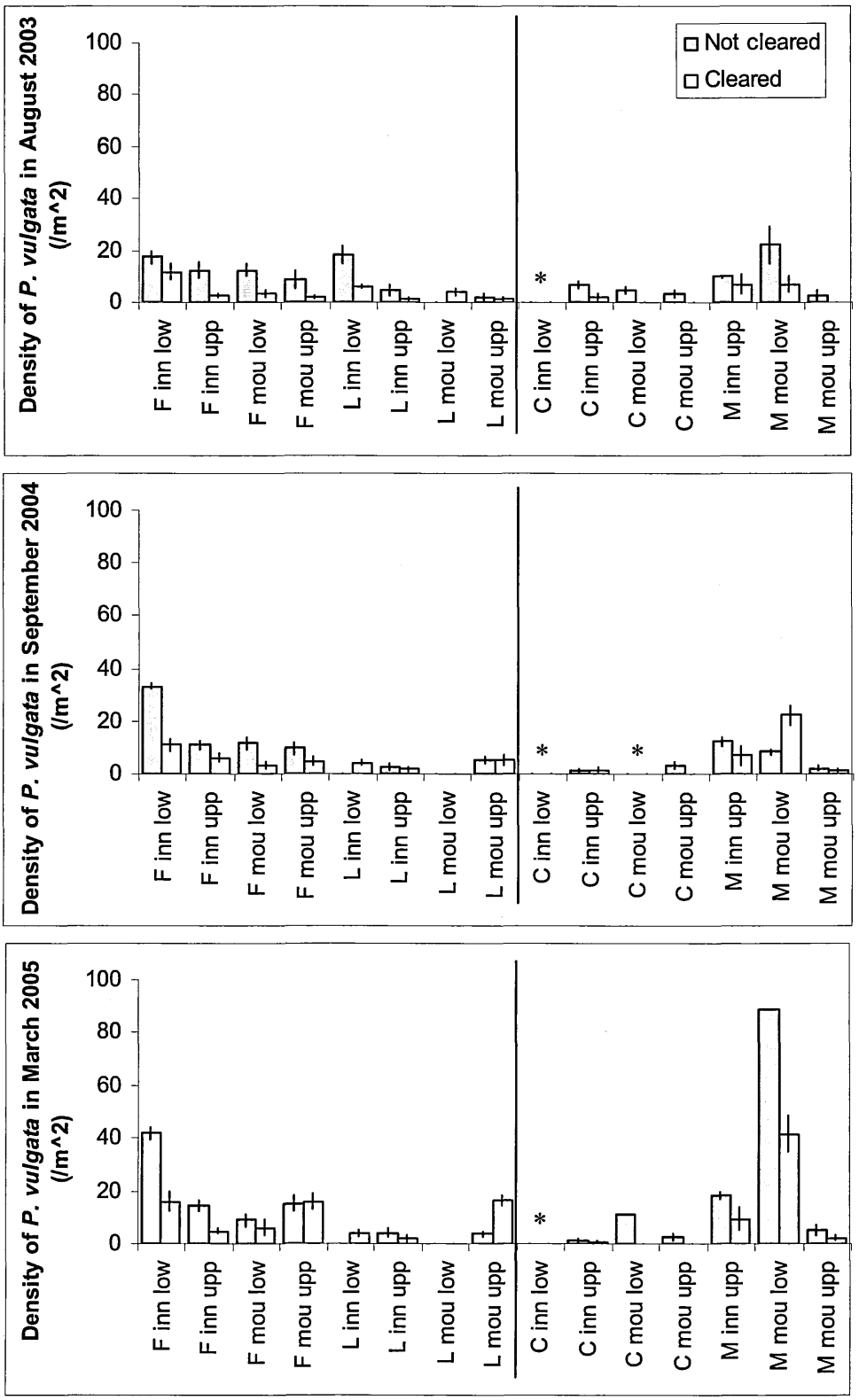


Figure 2.12 Average density of *P. vulgata* with corresponding 95% confidence intervals for August 2003, September 2004, and March 2005. * denotes sites which were not sampled.

2.3.2.5 *Nucella lapillus* density estimation from 30x30 cm quadrats

From the preliminary surveys of the four loch systems (see section 2.3.1), *N. lapillus* was found to be the ninth most abundant surveyed species found throughout the study area. Although *N. lapillus* was found within the 30x30 cm quadrats, they were not found in sufficient numbers at each site to determine any significant temporal or spatial patterns (Figure 2.13). The data from 30x30 cm quadrats records no *N. lapillus* at the inner site and very few at the mouth of Loch Caolisport as well as none on the upper shores of the inner site at Loch Fyne. This can be explained by sampling bias due to a small scale sampling area rather than a lack of animals. More *Nucella* were found at the lower shores of both regions. Within the Clyde system, more *N. lapillus* were found at the mouth of Lochs Fyne and Long which contrasted with the pattern at Loch Melfort where more animals were found at the inner site. These results should be treated with caution when taking into account the combined effect of the sampling bias and the findings over time.

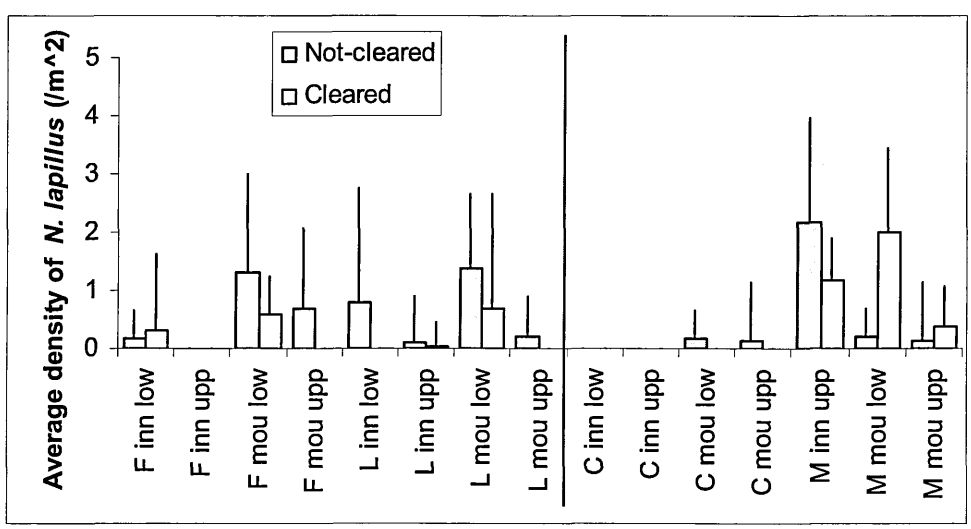


Figure 2.13 Average density of *N. lapillus* throughout the study period form March 2003 to June 2005 at all monitored sites. 95% confidence intervals are shown.

2.3.2.6 *Littorina littorea* density from 30x30 cm quadrats

Littorina littorea was the twelfth most abundant sampled species in the preliminary investigation (see section 2.3.1). The highest average density over the study period was found at Loch Long (mean = 25.3 m^{-2}, maximum = 77.8 m^{-2}) with densities at Lochs Fyne (mean = 5.1 m^{-2}, maximum = 15.3 m^{-2}), Caolisport (mean = 0.5 m^{-2}, maximum = 6.2 m^{-2}), and Melfort (mean = 0.5 m^{-2}, maximum = 5.6 m^{-2}) substantially lower (Figure 2.14).

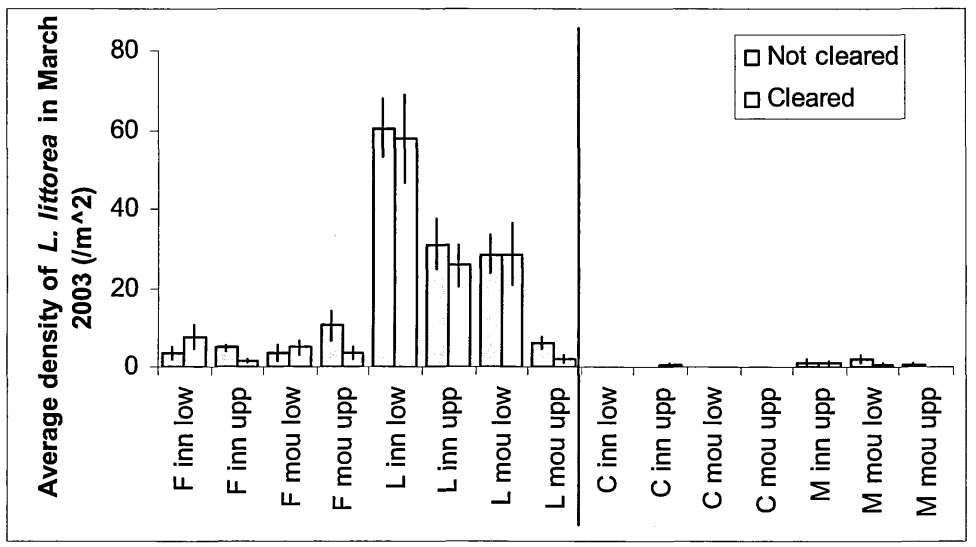


Figure 2.14 Average density of *L. littorea* for March 2003. Lower (low) and upper (upp) shores of the inner (inn) and mouth (mou) of each of Lochs Fyne (F), Long (L), Caolisport (C), and Melfort (M) are shown with corresponding 95% confidence intervals.

Highly significant differences in *L. littorea* density were found in relation to their position within the loch. Significantly greater densities were found at inner positions of Lochs Long and Melfort with Lochs Fyne and Caolisport having greater densities at the mouth of the loch (nested ANOVA, summary statistics, Table 2.8 and Appendix 2.13). A different pattern was found in August 2003 (Table 2.8 and Appendix 2.14) and September 2004 (Table 2.8 and Appendix 2.15) which showed greater densities at the inner positions of Lochs Long, Caolisport, and Melfort with Loch Fyne having a greater density at the mouth. March 2005 supported the findings of the summary statistics although no *L. littorea* were found in Loch Melfort (Table 2.8 and Appendix 2.15). Lochs in the Clyde had a significantly greater density at lower shore levels compared to lochs on the west coast which showed a greater density at upper shore levels (nested ANOVA, summary statistics, Table 2.8 and Appendix 2.13) although this was not supported by the monthly analysis.

Table 2.8 Summary of the significant nested ANOVA interactions for *L. littorea* densities. Significant results ($0.05 \geq *P > 0.01$; $0.01 \geq **P \geq 0.001$; $***P < 0.001$) are shown against the F ratio. Interactions significant at $P \leq 0.01$ are shown in bold. (++ denominator of the F test is zero)

	Summary	**August 2003**	**March 2004**	**September 2004**	**March 2005**
Loch(Region)	4.08	22.41*	++	5.05	1.04*
Position×Loch(Region)	19.61***	3.43*	0.05	3.93*	4.98**
Height×Loch(Region)	3.33*	1.38	<0.01		1.30

2.3.2.7 *Littorina* species density from 30x30 cm quadrats

Littorina species include all Littorinids (*L. obtusata*, *L. mariae* Sacchi, and *L. saxatilis*) with the exception of *Littorina littorea*. As with *L. littorea* (see section 2.3.2.6), the greatest density of *Littorina* species was found at Loch Long (mean = 10.4 m^{-2}, maximum = 55.6 m^{-2}) with densities in Lochs Fyne (mean = 0.4 m^{-2}, maximum = 6.3 m^{-2}), Caolisport (mean = 1.8 m^{-2}, maximum = to 38.3 m^{-2}), and Melfort (mean = 1.7 m^{-2}, maximum = to 33.3 m^{-2}) substantially lower (Figure 2.15).

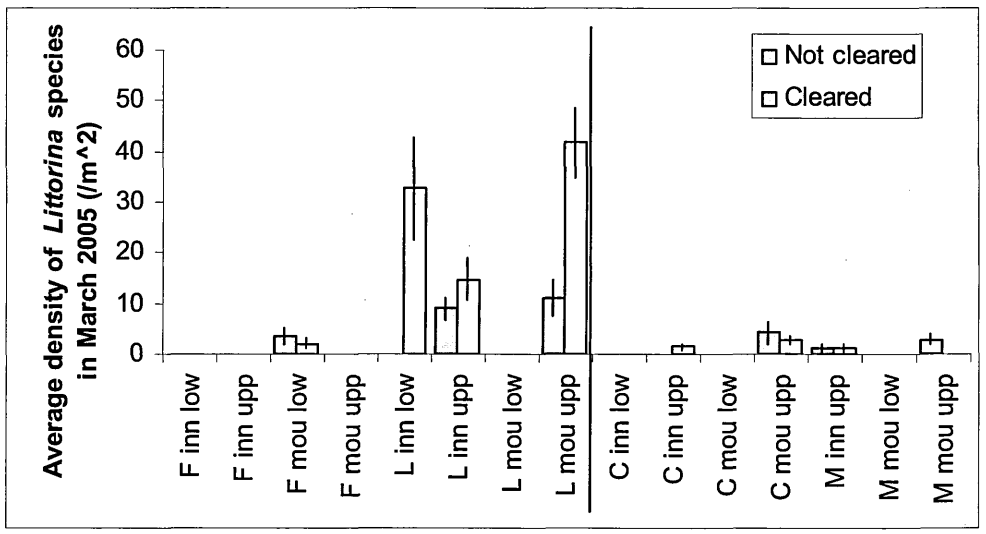


Figure 2.15 Average density of *Littorina* species for March 2005. Lower (low) and upper (upp) shores of the inner (inn) and mouth (mou) of each of Lochs Fyne (F), Long (L), Caolisport (C), and Melfort (M) are shown with corresponding 95% confidence intervals.

A significantly greater density of *Littorina* species were found at the upper shore (nested ANOVA, summary statistics, Table 2.9 and Appendix 2.16) although this was not supported by the monthly analysis. Lower shores in the Clyde were found to have a greater density with no *Littorina* species found at this height in the west coast during

September 2004 (Table 2.9 and Appendix2.19). Two years from the start of the experiment in March 2005, density was found to differ significantly with position and height (Table 2.9 and Appendix 2.18). Upper shores were found to have a significantly greater density at the mouth of lochs but at inner positions, density was greater at lower shore heights. Greater densities at cleared areas were noted for Lochs Long and Caolisport with *Littorina* species favouring areas which were not cleared in Lochs Fyne and Melfort (nested ANOVA; summary statistics, Appendix 2.16; March 2004, Appendix 2.17; Table 2.9).

Table 2.9 Summary of the significant nested ANOVA interactions for *Littorina* species densities. Significant results ($0.05 \geq *P > 0.01$; $0.01 \geq **P \geq 0.001$; $***P < 0.001$) are shown against the F ratio. Interactions significant at $P \leq 0.01$ are shown in bold.

	Summary	**August 2003**	**March 2004**	**September 2004**	**March 2005**
Height	9.23*	0.13	0.27	0.36	<0.01
Region×Height	5.85	2.90	1.28	4.48*	0.47
Position×Height	<0.01	0.20			4.30*
Position×Cleared	1.75	1.26	1.51	2.70	4.83*
Position×Loch(Region)	2.47	6.75**	16.18***	1.71	1.07
Cleared×Loch(Region)	3.40*	0.53	5.84*	3.06	2.54
Region×Position×Cleared	0.40	0.66	8.13**	0.32	<0.01

2.3.3 Density variation in *Semibalanus balanoides*

Semibalanus balanoides was found throughout the study area at both upper and lower shores. The density of *S. balanoides* was found to fluctuate over time with each settlement and corresponding mortality (Figure 2.16). Throughout the study three settlements were observed in 2003, 2004, and 2005. Peaks in density were recorded during May 2003, March 2004, and June 2005 at both lochs in the Clyde system. This pattern corresponded with density peaks in Lochs Caolisport and Melfort with the exception of the second density peak in Loch Melfort which was recorded during September 2003. Settlement was estimated to occur in mid to late April in the Clyde system and early April on the west coast. Loch Long had the highest average density of 6.3 individuals/cm^2 (range 1.2 to 22.3 cm^{-2}) with Lochs Fyne (mean = 4.5 cm^{-2}, range 0.7 to 8.2 cm^{-2}), Caolisport (mean = 3.7 cm^{-2}, range 0.7 to 7.9 cm^{-2}), and Melfort (mean = 5.0 cm^{-2}, range 0.5 to 11.9 cm^{-2}) having slightly lower densities. Regional differences in density were found during August 2003 (Table 2.10 and Appendix 2.20) and September 2004 (Table 2.10 and Appendix 2.21). A greater density of *S. balanoides* was found on the west coast in August with a shift in density to the Clyde one year later in September. Inner sites of Lochs Fyne and Caolisport and mouth sites of Lochs Long and Melfort were found to have significantly greater densities (summary statistics, Table 2.10 and Appendix 2.19) although by March 2004 the inner site at Lochs Long and Caolisport and the mouth of Loch Melfort were found to have a greater density (Table 2.10 and Appendix 2.20).

Density of *S. balanoides* at upper and lower shores was found to significantly differ throughout the study period. During August 2003 the lower shore was found to have a greater density in Loch Fyne and both lochs of the west coast (Table 2.10 and Appendix 2.20). This higher density at the lower shore on the west coast was noted one year from the start of the experiment in March 2004 with the Clyde having a higher density at the upper shore (Table 2.10 and Appendix 2.20). The lower shores of inner and mouth positions were found to have a greater density in September 2004 (Table 2.10 and Appendix 2.21) with the upper shore found to have a higher density in both regions two years from the start of the experiment in March 2005 (Table 2.10 and Appendix 2.21).

Table 2.10 Summary of the significant nested ANOVA interactions for *S. balanoides* densities. Significant results ($0.05 \geq *P > 0.01$; $0.01 \geq **P \geq 0.001$; ***$P < 0.001$) are shown against the F ratio. Interactions significant at $P \leq 0.01$ are shown in bold. (++ denominator of the F test is zero)

	Summary	**August 2003**	**March 2004**	**September 2004**	**March 2005**
Region	2.18	6.73*	++	6.41*	0.24
Position	0.60	4.15	1.61	8.02*	0.78
Region×Height	0.55	0.26	30.57	0.13	4.27*
Position×Height	3.52	1.43		13.51**	0.25
Position×Loch(Region)	5.08**	0.19	4.60*	0.61	2.70
Height×Loch(Region)	1.78	9.69***	0.59		0.05
Region×Position×Cleared		7.83**	1.28	1.93	3.35

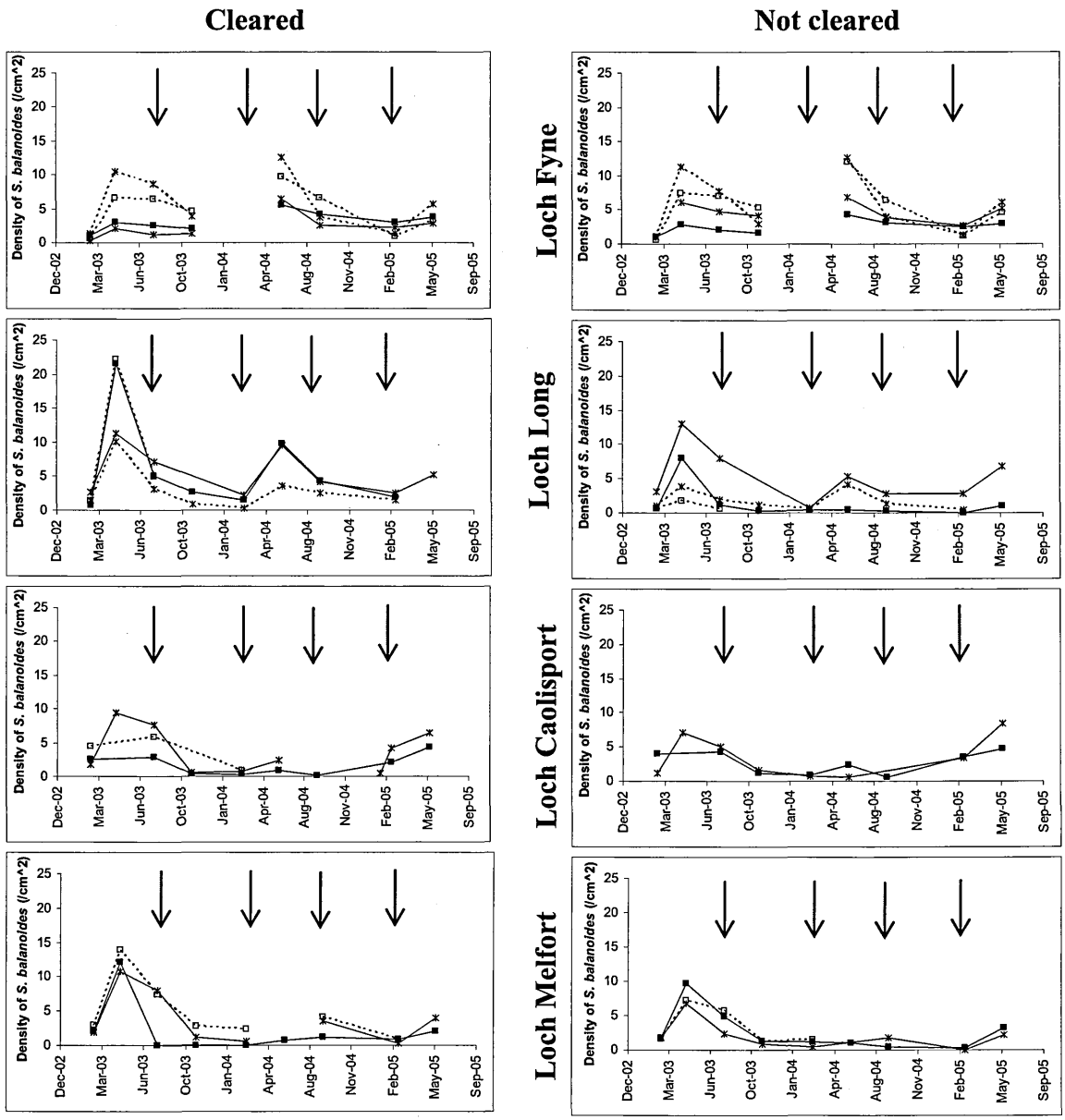


Figure 2.16 Density (number/cm^2) of *S. balanoides* from cleared and non-cleared areas of four loch systems. Inner (star) and mouth (square) sites are shown with solid lines for upper shore quadrats and dashed lines for lower shore quadrats. Values recorded during March 2003 at cleared areas correspond to densities prior to the area being cleared. Downward pointing arrows indicate time periods where nested ANOVAs were carried out.

2.3.4 *Semibalanus balanoides* size

Lengths of *S. balanoides* were measured for the three settlement periods in 2003, 2004, and 2005 and of individuals previously recruited to the population prior to the start of the experiment in 2003 (see Figure 2.17 for the 2003 settlement and Figure 2.18 for the 2004 settlement). The largest mean lengths were found in Loch Fyne in the established population and the population from the 2003 settlement (Table 2.11). Although the largest mean lengths for the 2004 and 2005 settlements were found in Loch Melfort, the largest individuals of these settlements were found in Loch Fyne. The largest *S. balanoides* (5.08 mm) was measured at the inner site of Loch Long at the lower shore from the established population. The largest barnacle of the 2003 settlement (4.70 mm) was measured on the upper shore at the inner site of Loch Caolisport in March 2005 with the largest barnacle of that settlement in Loch Long (3.97 mm) measured at the mouth on the upper shore during June 2005 (Table 2.11). The smallest mean length was found on the west coast for the established population (2.51 mm at Loch Caolisport), 2003 settlement (1.70 mm at Loch Melfort), and 2005 settlement (0.74 mm at Loch Caolisport) with the smallest mean length of the 2004 settlement found at Loch Long (1.69 mm).

Table 2.11 Mean lengths (mm), from time of settlement to the end of the experiment, of *S. balanoides* at each loch for four populations with their corresponding length ranges (mm). Populations included the three observed settlements and the established population.

	Settlement			
Loch	**Established**	**2003**	**2004**	**2005**
Fyne	3.36 (2.13-4.99)	2.27 (0.78-4.12)	1.78 (0.51-3.67)	1.24 (0.97-1.62)
Long	3.31 (2.21-5.08)	2.00 (0.57-3.97)	1.69 (0.55-2.76)	0.97 (0.44-1.38)
Caolisport	2.51 (0.60-4.10)	2.07 (0.84-4.70)	1.78 (0.66-2.99)	0.74 (0.47-1.17)
Melfort	2.51 (1.51-4.28)	1.70 (0.53-4.64)	1.80 (0.44-3.26)	1.24 (1.06-1.54)

As in previous sections monthly analysis was carried out in order to corroborate the findings of the summary statistics. When examining *S. balanoides* lengths it was found that the summary statistics were a good representation for all three settlements and those individuals measured in the established population (see Appendices 2.23 and 2.24). The lengths of the established population were found to be significantly larger in the Clyde system to those on the west coast (Table 2.12 and Appendix 2.22) although this trend was not found in the subsequent three settlements. Position within lochs were found to be highly significant in the established population (Table 2.12 and Appendix 2.22) and the three settlements (2003 settlement, Table 2.12, Figure 2.17 and Appendix 2.22; 2004 settlement, Table 2.12, Figure 2.18 and Appendix 2.23; 2005 settlement, Table 2.12 and Appendix 2.23). Larger *S. balanoides* were found at the inner site of Loch Caolisport for all settlements and at Loch Fyne with the exception of the 2005 settlement which had larger barnacles at the mouth of the loch. Only the established population at Loch Melfort had significantly larger barnacles at the inner site with larger barnacles found at the mouth for settlements during 2003, 2004, and 2005. Larger

barnacles were found at the inner site of Loch Long from the 2003 and 2004 settlements with the established population and the 2005 settlement found to have larger barnacles at the mouth of the loch. The 2005 settlement showed additional differences in lengths with height up the shore found to be a significant factor. Larger barnacles were found on the lower shore of the Clyde and the upper shore of the west coast with larger barnacles also found at the lower shores of both the inner and mouth sites (Table 2.12 and Appendix 2.23).

Table 2.12 Summary of the significant nested ANOVA interactions from the summary statistics for *S. balanoides* lengths. Significant results ($0.05 \geq *P > 0.01$; $0.01 \geq **P \geq 0.001$; $***P < 0.001$) are shown against the F ratio. Interactions significant at $P \leq 0.01$ are shown in bold.

		Settlement		
	Established	**2003**	**2004**	**2005**
Region	88.33***	0.56	0.01	1.03
Region×Height	3.39	0.04	0.47	23.35***
Position×Height	0.02	0.63	0.46	9.64**
Position×Cleared		3.29	0.11	6.35*
Position×Loch(Region)	11.88***	9.49***	6.40**	17.57***

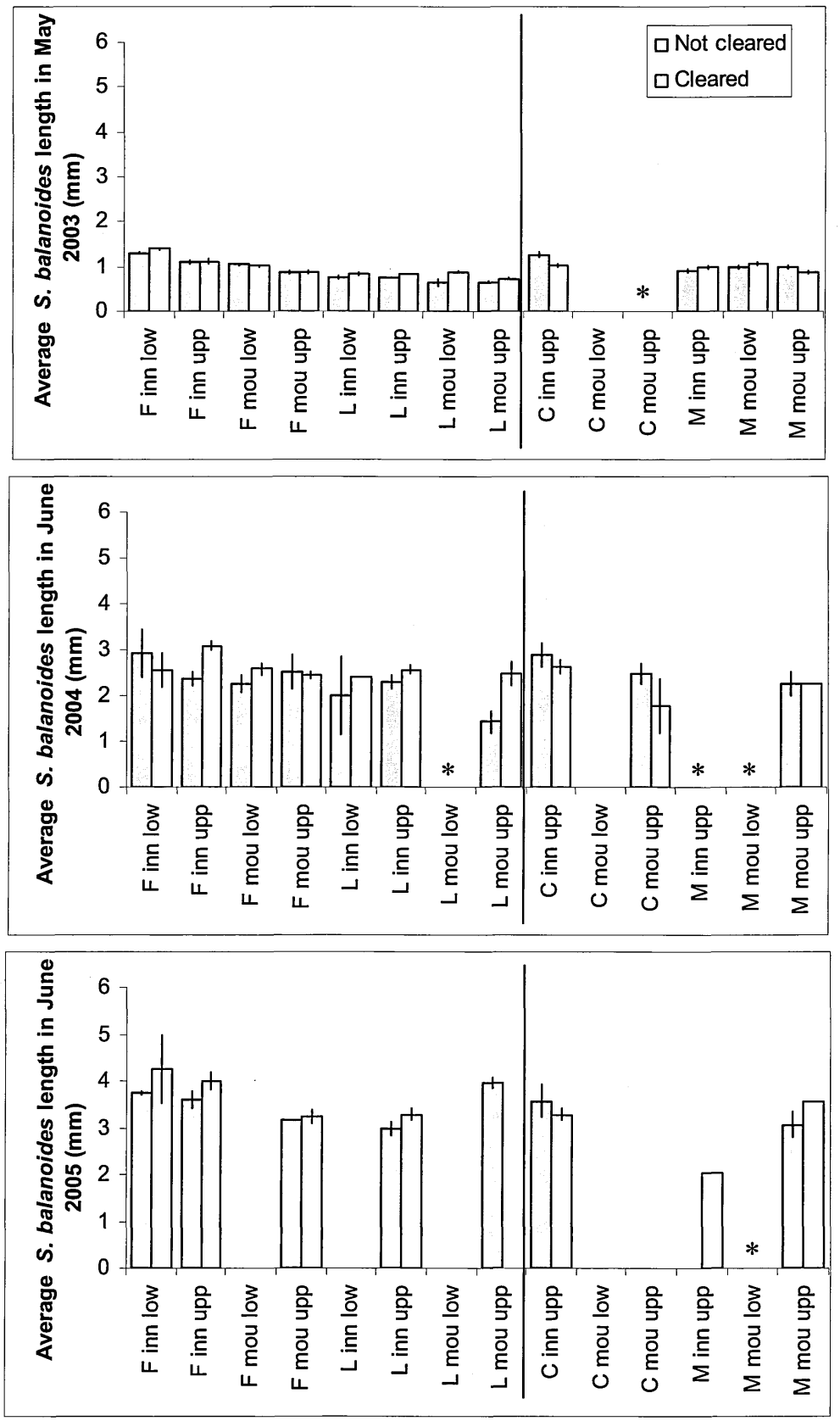


Figure 2.17 Average length of the 2003 *S. balanoides* settlement with corresponding 95% confidence intervals. * denotes sites which were not sampled.

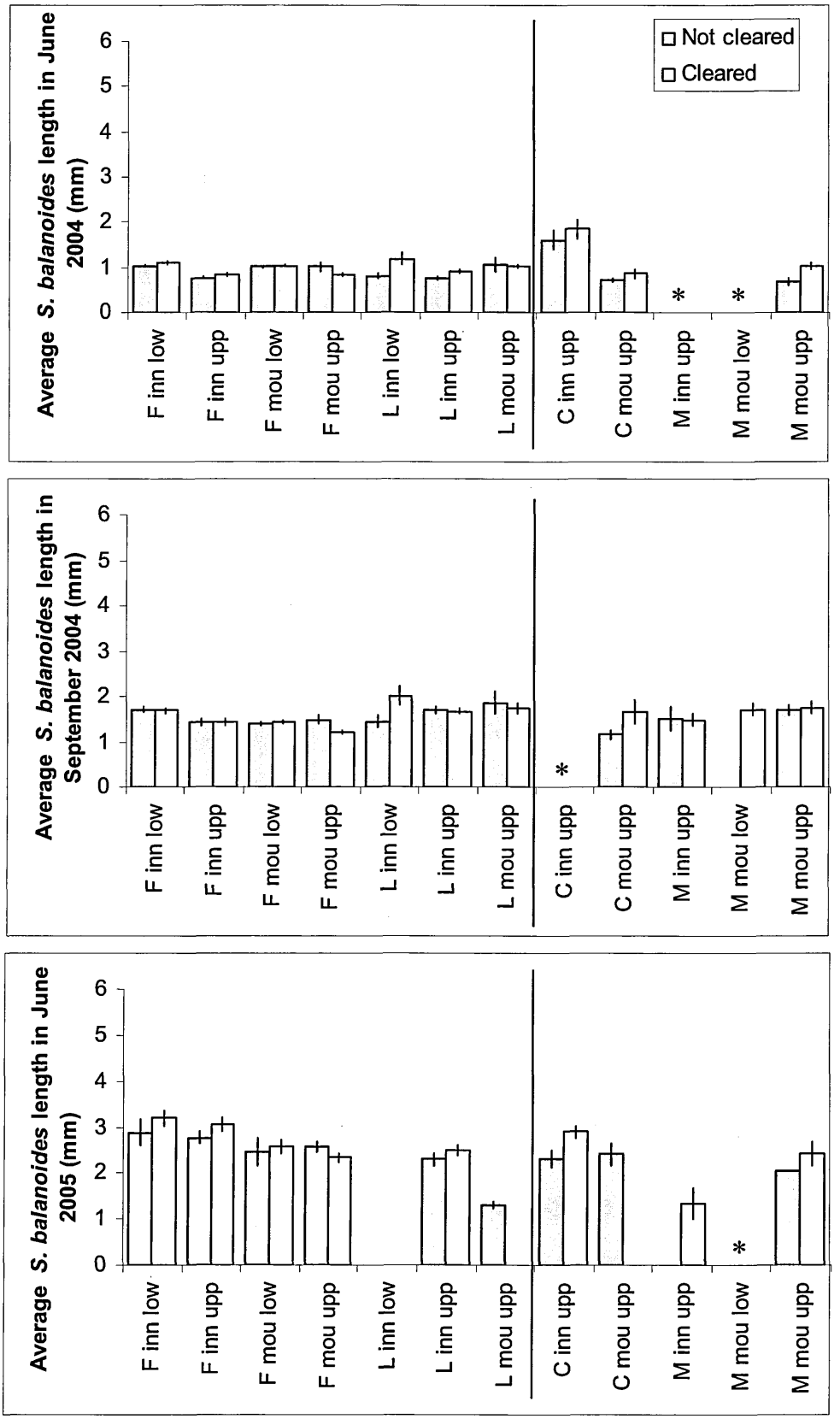


Figure 2.18 Average length of the 2004 *S. balanoides* settlement with corresponding 95% confidence intervals. * denotes sites which were not sampled.

Growth rates of the 2003 *S. balanoides* population are shown to enable comparisons with other studies (Figure 2.19 to Figure 2.22). The fastest growth rate of 0.14 mm/month was recorded at the mouth of Loch Long at MHWN with an initial length of 0.73 ±0.02 mm measured in May 2003. The lower shore of Loch Long was found to have the fastest growth rate for inner sites of 0.13 mm/month with an initial length of 0.84 ±0.03 mm measured in May 2003. The slowest growth rates of the mouth (0.06 mm/month, initial length of 1.07 ±0.03 mm) and inner (0.04 mm/month, initial length of 0.99 ±0.03 mm) positions were both measured at Loch Melfort on the lower and upper shores respectively.

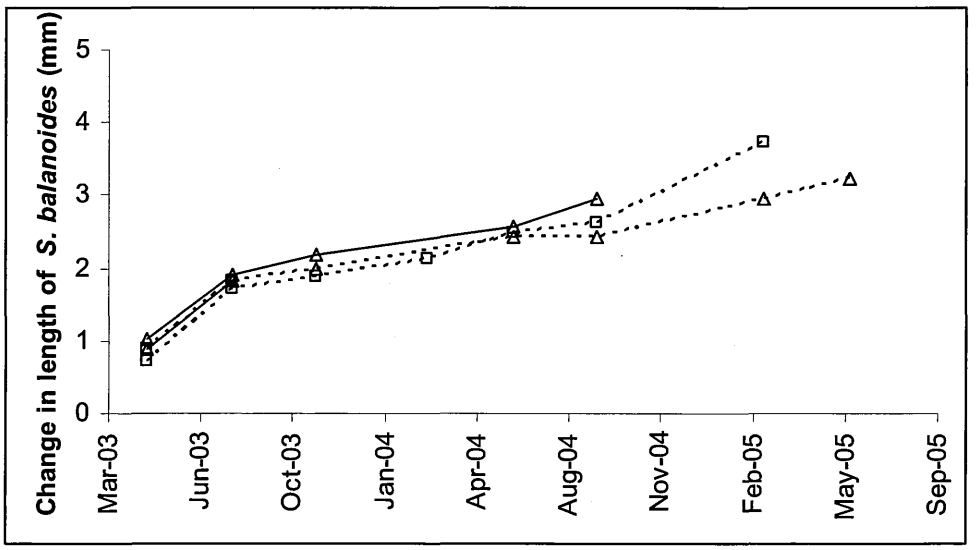


Figure 2.19 Growth in *S. balanoides* as change in average size at the upper (broken line) and lower (solid line) shores at the mouth of Lochs Fyne (triangle) and Long (square).

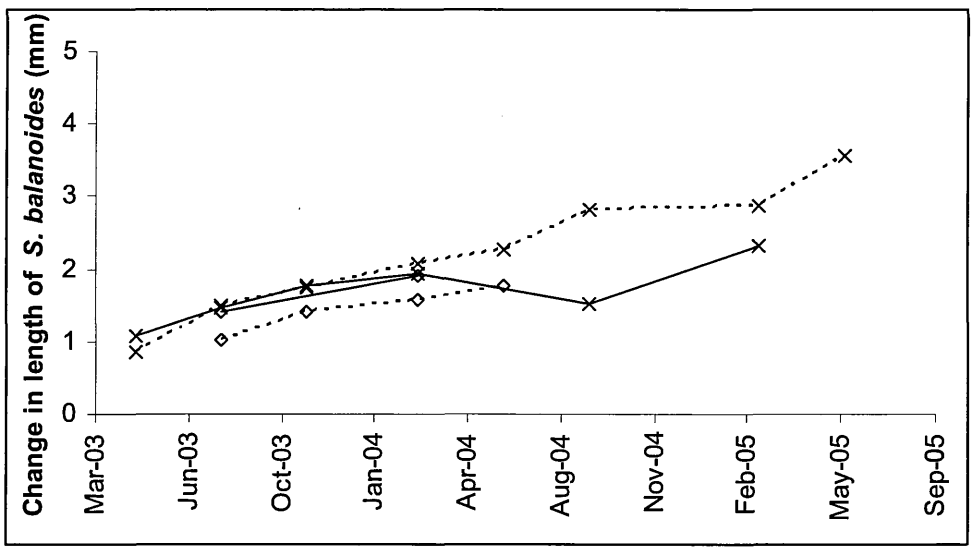


Figure 2.20 Growth in *S. balanoides* as change in average size at the upper (broken line) and lower (solid line) shores at the mouth of Lochs Caolisport (diamond) and Melfort (cross).

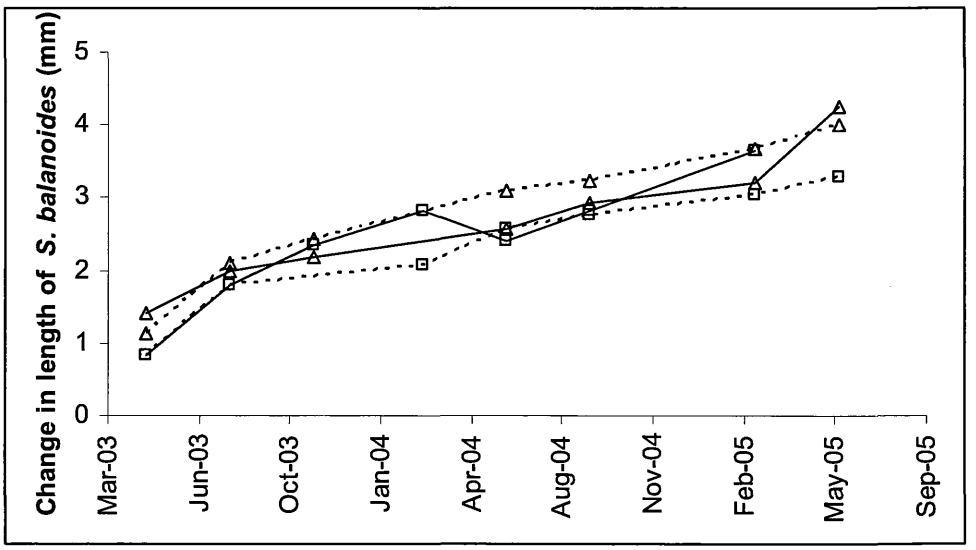


Figure 2.21 Growth in *S. balanoides* as change in average size at the upper (broken line) and lower (solid line) shores at the inner site of Lochs Fyne (triangle) and Long (square).

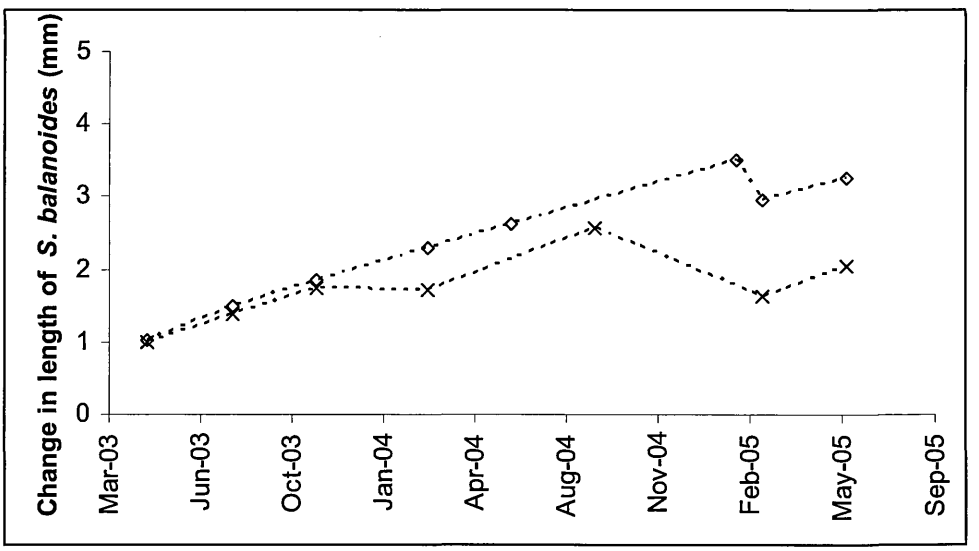


Figure 2.22 Growth in *S. balanoides* as change in average size at the upper (broken line) and lower (solid line) shores at the inner site of Lochs Caolisport (diamond) and Melfort (cross).

2.3.5 Density variation in *Chthamalus montagui*

Two settlement periods were recorded for *C. montagui* between August and November of 2003 and 2004. *Chthamalus montagui* was found at upper shore heights throughout the study area (Table 2.13). More *C. montagui* were found on the west coast with the greatest number of this barnacle species found in Loch Melfort. Loch Fyne had a high abundance of *C. montagui* in the Clyde with few found in Loch Long. The density of this species was found to be relatively stable over time which can be seen from non-cleared areas of the west coast and Clyde (Figure 2.23 and Figure 2.24, respectively). Densities within cleared areas were slow to recover in all lochs with the exception of Loch Melfort (nested ANOVA, summary statistics $F_{2,25} = 3.74$, $P = 0.038$, Appendix 2.24) which showed a rapid increase in *C. montagui* density between March and September 2004 (Figure 2.23). By March 2005 a significantly greater density of *C. montagui* was found at Loch Melfort compared with the other three lochs (nested ANOVA, $F_{2,18} = 5.94$, $P = 0.010$, Figure 2.23, and Appendix 2.24).

Table 2.13 Number of *C. montagui* found at each loch from two settlement periods and the established population expressed as a percentage of the overall settlement period with densities shown in brackets (number cm^{-2}).

	Settlement		
Loch	**Established**	**2003**	**2004**
Fyne	39.63 (2.13)	4.68 (0.19)	36.59 (0.35)
Long	2.40 (0.27)	2.22 (0.35)	18.29 (0.83)
Caolisport	28.02 (0.86)	14.64 (0.36)	37.80 (0.33)
Melfort	29.95 (2.08)	78.45 (2.76)	7.32 (0.27)

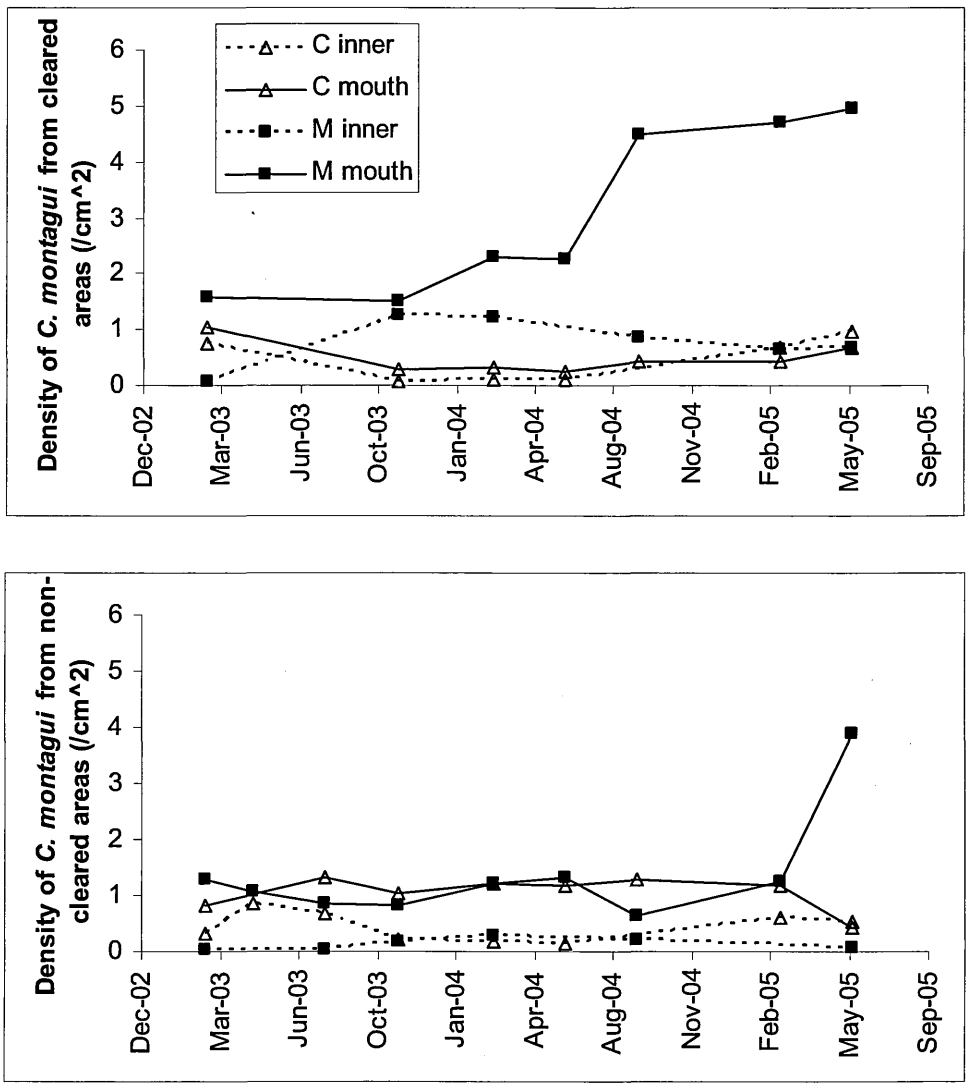


Figure 2.23 Density of *C. montagui* on the west coast from Lochs Caolisport (C) and Melfort (M). Values recorded during March 2003 at cleared areas correspond to densities prior to the area being cleared.

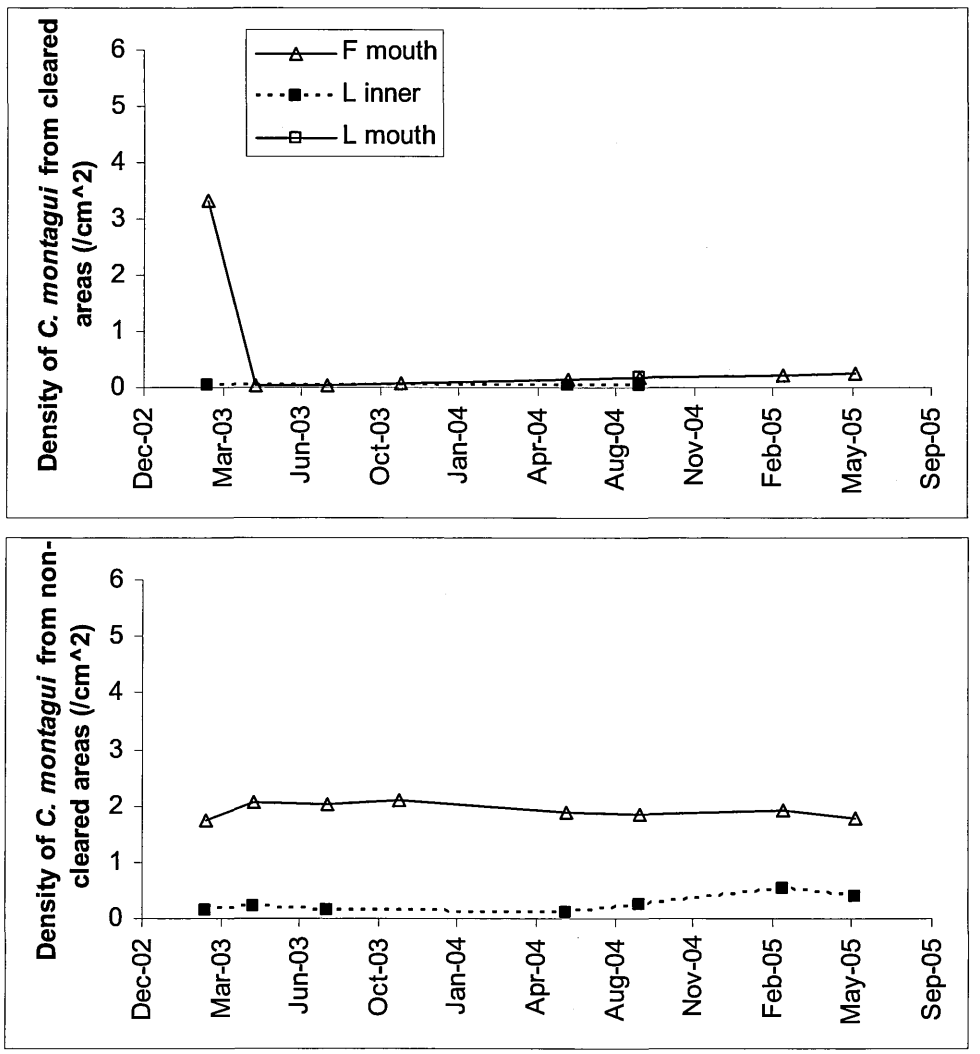


Figure 2.24 Density of *C. montagui* in the Clyde system from Lochs Fyne (F) and Long (L). Values recorded during March 2003 at cleared areas correspond to densities prior to the area being cleared.

2.3.6 *Chthamalus montagui* size

Lengths of *C. montagui* were measured for the established population (Figure 2.25) before the start of the experiment and two settlement periods occurring in 2003 (Figure 2.26) and 2004 (Figure 2.27, see Table 2.14 for mean lengths and corresponding ranges). Loch Caolisport was found to have the largest overall mean operculum length of 1.68 mm (range 0.58 to 2.80 mm) and Loch Long the smallest (mean = 1.28 mm, 0.48 range to 1.96 mm). The largest measured individual was from the 2003 settlement, measured 3.62 mm in length and found at the mouth of Loch Fyne during September 2004. This was larger than the largest barnacle measured in the established population which measured 3.21 mm and was found at the mouth of Loch Caolisport during June 2005 (Table 2.14).

Table 2.14 Mean lengths of *C. montagui* at each loch for three populations with their corresponding length ranges (mm). Populations included the two observed settlements and the established population.

	Settlement		
Loch	**Established**	**2003**	**2004**
Fyne	2.03 (1.49-2.61)	1.37 (0.41-3.62)	1.21 (0.47-2.61)
Long	1.54 (1.05-1.96)	0.96 (0.48-1.31)	0.94 (0.67-1.26)
Caolisport	2.19 (1.19-3.21)	1.38 (0.60-2.68)	1.23 (0.44-2.35)
Melfort	2.14 (1.85-2.58)	0.90 (0.34-1.97)	0.58 (0.44-0.67)

As with *S. balanoides* (see section 2.3.4) summary statistics were used to examine differences in *C. montagui* lengths for the established population and the two settlement periods (see Appendix 2.25 for the summary statistics results). Although summary statistics are regarded as a good representation of the data, no statistical differences in the summary statistics were found in either of the two settlements or the established population. For this reason it was felt that monthly analysis should be combined with the summary statistics for the established population (Appendix 2.26) and the 2003 settlement (Appendix 2.27). Examining the monthly analysis it was found that significantly larger barnacles were found at the mouth of lochs in August 2003 and March 2005 (Table 2.15) for the established population and March 2005 (Table 2.15) for the 2003 settlement.

Regional differences were found in *C. montagui* lengths with larger individuals found along the west coast in the established population during August 2003 and September 2004 (Figure 2.25, Table 2.15, and Appendix 2.26). Loch Caolisport was found to have the largest barnacles in March 2005 for both the established (Table 2.15 and Appendix 2.26) and the 2003 settlement (Figure 2.26, Table 2.15, and Appendix 2.27) with Loch Long having the smallest barnacles during March 2005 of the established population (Table 2.15 and Appendix 2.26) and September 2004 of the 2003 settlement (Table 2.15 and Appendix 2.27) with the latter date and settlement showing larger barnacles in Loch Fyne.

Table 2.15 Summary of the significant nested ANOVA interactions for *C. montagui* lengths of the established population and the 2003 and 2004 settlements. Significant results ($0.05 \geq *P > 0.01$; $0.01 \geq **P \geq 0.001$; $***P < 0.001$) are shown against the F ratio. Interactions significant at $P \leq 0.01$ are shown in bold.

	Summary	**August 2003**	**March 2004**	**September 2004**	**March 2005**
Established					
Region	43.41	29.17***		8.56**	0.81
Loch(Region)	0.26	0.20		1.18	3.48*
Position	2.35	5.00*	257.85*	0.40	13.20***
2003 settlement					
Loch(Region)	0.78			10.32***	4.07*
Position	0.06		2.73	1.12	31.14***
Cleared	0.41		1.16	5.57*	0.31
Position×Cleared	0.16		0.77	2.41	11.19**
2004 settlement					
Loch(Region)	1.81			0.46	3.64*
Cleared	0.05			6.58*	0.69

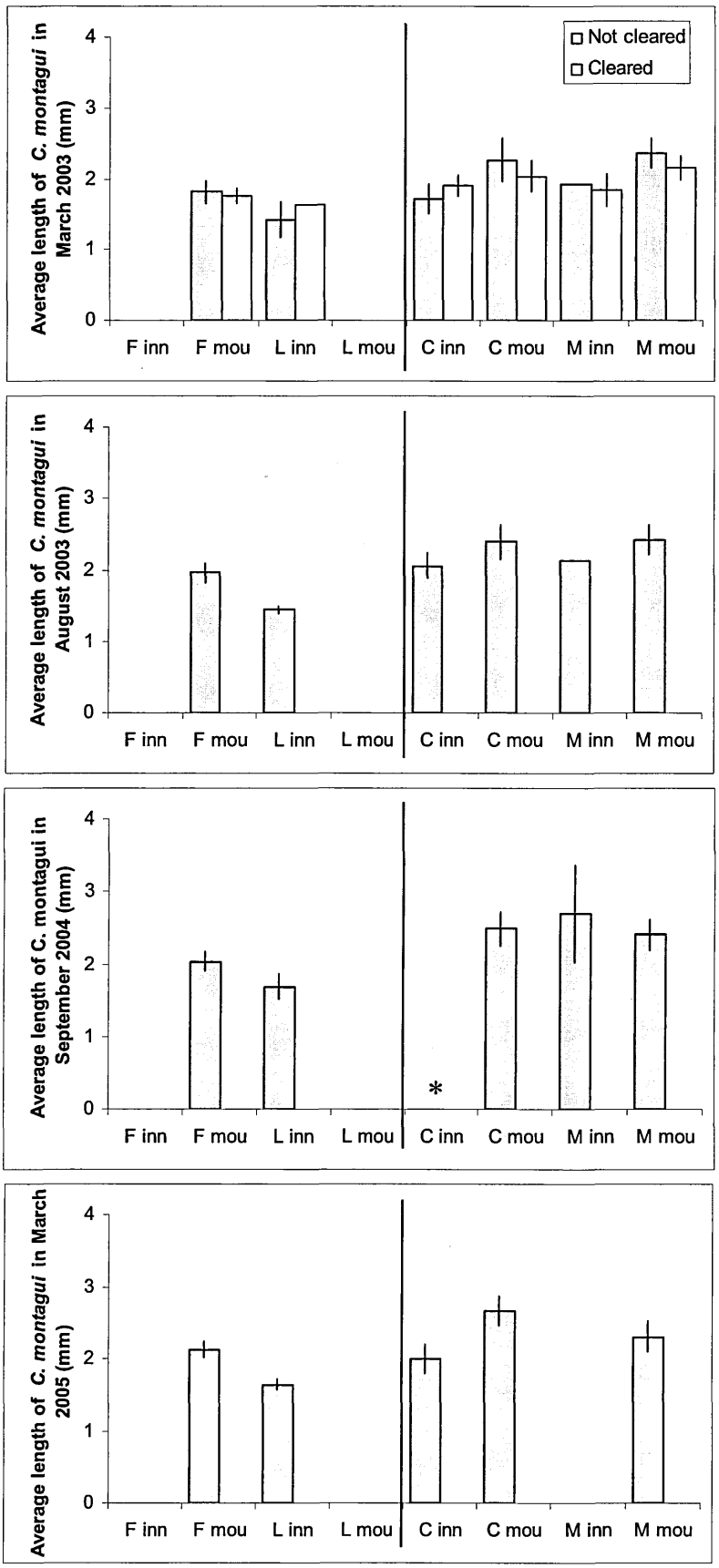


Figure 2.25 Average length of *C. montagui* from individuals which recruited to the population prior to the start of the experiment. 95% confidence limits are shown. * denotes sites which were not sampled.

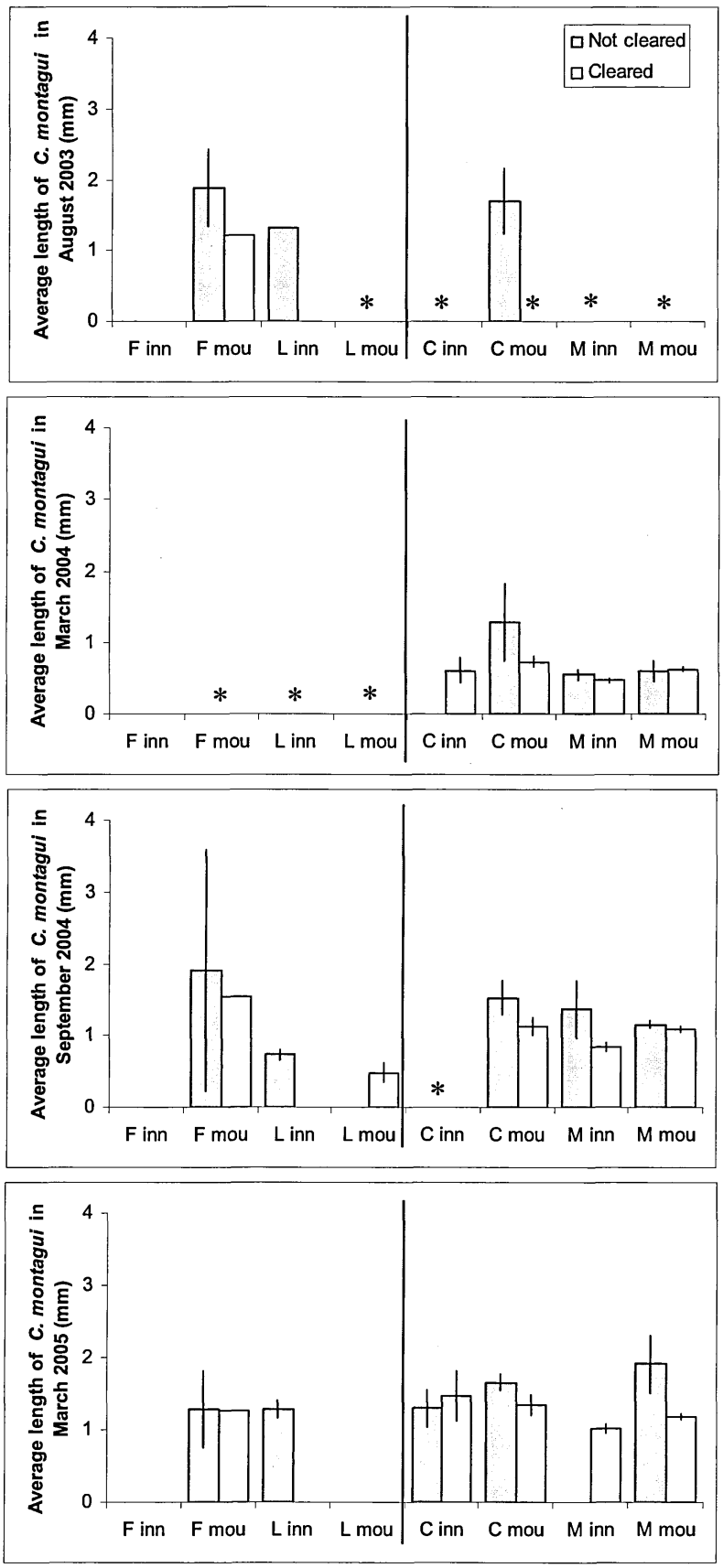


Figure 2.26 Average length of *C. montagui* from the 2003 settlement with 95% confidence limits shown. * denotes sites which were not sampled.

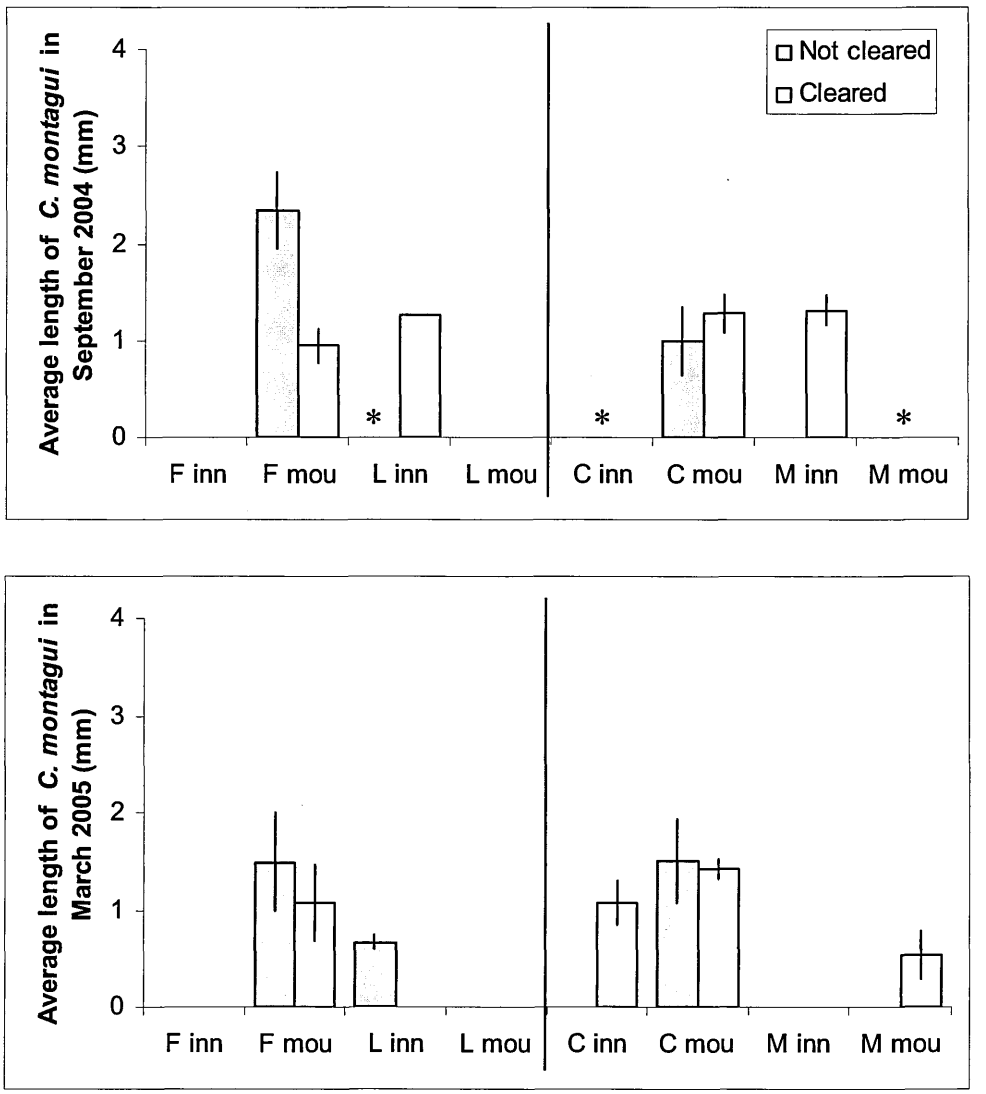


Figure 2.27 Average length of *C. montagui* from the 2004 settlement with 95% confidence limits shown. * denotes sites which were not sampled.

Growth rates of the *C. montagui* population varied in the 2003 and 2004 settlements (Figure 2.28 and Figure 2.29). The inner site of Loch Caolisport was found to have the fastest growth rate of 0.070 mm/month with an average initial length measured in March 2004 of 0.60 ±0.18 mm for the 2003 settlement. The fastest growth rate of the 2004 settlement (0.063 mm/month) was found at the mouth of Loch Fyne with an initial length measured in June 2004 of 0.74 ±0.22 mm. The slowest growth rates were found at the mouth of Loch Fyne (0.016 mm/month, initial length of 1.04 mm measured in November 2003, n = 1) for the 2003 settlement and the mouth of Loch Caolisport (0.028 mm/month, initial length of 0.81 ±0.10 mm measured in March 2004) for the 2004 settlement.

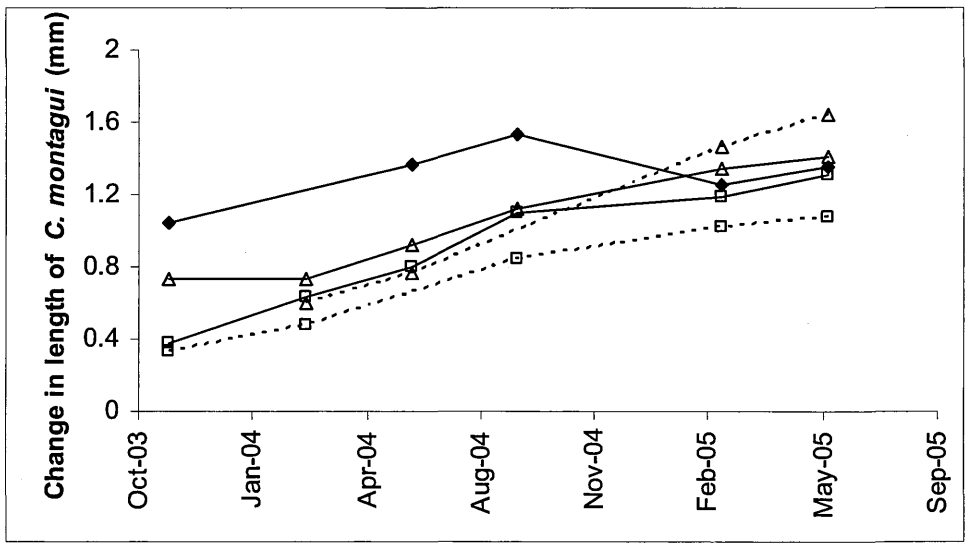


Figure 2.28 Growth in *C. montagui* as change in size from the 2003 settlement. Mouth (solid lines) and inner (broken lines) sites are shown for Lochs Fyne (filled diamond), Caolisport (triangle), and Melfort (square).

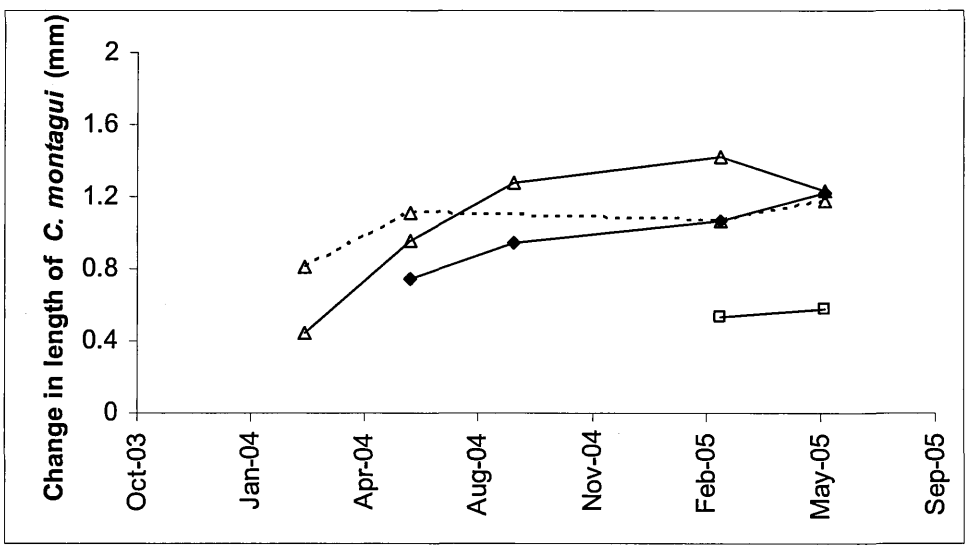


Figure 2.29 Growth in *C. montagui* as change in size from the 2004 settlement. Mouth (solid lines) and inner (broken lines) sites are shown for Lochs Fyne (filled diamond), Caolisport (triangle), and Melfort (square).

2.3.7 The occurrence of *Chthamalus stellatus* and *Elminius modestus* within Lochs Long, Caolisport, and Melfort

Chthamalus stellatus and *E. modestus* were both found within the sampling area but in relatively small numbers. A total of 125 *C. stellatus* and 23 *E. modestus* were measured which corresponded with 25 and 14 individuals, respectively. This compared with 26 948 measured *S. balanoides* and 2 570 *C. montagui*. Both species were only noted at upper shore heights.

Chthamalus stellatus were mainly found on the west coast with only one individual measured in the Clyde, at the inner site of Loch Long. On the west coast they were found at both the inner (n = 2) and mouth (n = 14) sites of Loch Caolisport and at the mouth (n = 8) of Loch Melfort but none were found at the inner site of Loch Melfort. Settlement of *C. stellatus* was not observed at any of the locations with all measured individuals having recruited prior to the start of the experiment. The smallest *C. stellatus* was 0.78 mm and the largest was 3.68 mm (mean of 2.09 mm). Both these individuals were found at the mouth of Loch Caolisport which also had the highest density of 0.39 *C. stellatus*/cm^2. Mean population length change at the mouth of Loch Caolisport was 0.57 mm after 27 months (0.54 mm after two years) from an initial mean length of 1.84 mm (Figure 2.30).

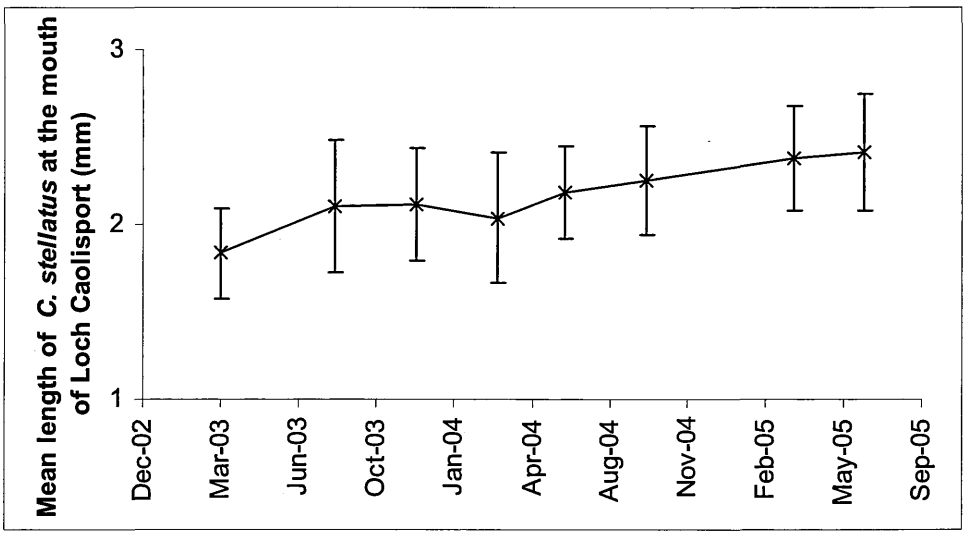


Figure 2.30 Mean population length change from March 2003 to July 2005 of *C. stellatus* at the mouth of Loch Caolisport with corresponding 95% confidence intervals.

Elminius modestus were mainly found in the Clyde system at the inner site of Loch Long (n = 11) with only two individuals found at the mouth of Loch Melfort and one at the inner site of the same loch. Three individuals were measured at the mouth of Loch Long in areas which were later scraped clean but no further recruitment of *E. modestus* was noted at this location. The smallest *E. modestus* was 0.90 mm and the largest was 2.45 mm (mean 1.51 mm). Both individuals were found in Loch Melfort and measured in June 2005 at the mouth site and September 2004 at the inner site, respectively. At the inner site of Loch Long, the smallest *E. modestus* was 1.04 mm (measured in March 2005) and the largest was 2.01 mm measured in June 2005 (mean 1.54 mm).

All the major significant interactions for each species were summarised (Table 2.16).

Table 2.16 A summary of the major significant effects for barnacle and macroalgal cover, species densities, and barnacle species lengths. Interactions were chosen where three or more factors were found to be significant at $P \leq 0.01$. Abbreviations for interactions are: R = region, P = loch position, H = shore height, L = loch.

Factors	R	R×H	P×H	P×L(R)	H×L(R)
Cover					
Barnacle	✓	✓		✓	✓
Macroalgae		✓		✓	
Density					
P. vulgata			✓	✓	✓
L. littorea				✓	
Littorina species				✓	
S. balanoides			✓	✓	✓
Length					
S. balanoides (established)	✓			✓	
S. balanoides (2003 settlement)				✓	
S. balanoides (2005 settlement)		✓	✓	✓	
C. montagui (established)	✓				

2.4 Discussion

2.4.1 Comparisons of Clyde and west coast communities

Regional differences were seen in the preliminary survey and in the long term analysis of barnacle and macroalgal cover. Macroalgae and filter feeders were the major organisms determining regional differences. Abundant filter feeders characterised the Clyde system and macroalgae the west coast. The mussel, *M. edulis*, and the barnacle, *S. balanoides*, dominated the Clyde with the two Chthamalid barnacles found to favour the west coast. Upwelling intensity, currents, and phytoplankton concentration were major determinants of between-site differences in the abundance of sessile invertebrates and macrophytes, on the South Island of New Zealand, (Menge *et al.* 1999). High abundances of sessile invertebrates were found to occur on rocky shores adjacent to a region characterised by gyres and eddies that may both concentrate zooplankton and phytoplankton, transporting them to shore during upwelling relaxations (Menge *et al.* 1999). Their results suggest that continental west coast up-welling regions, of New Zealand, with high phytoplankton productivity and particulate abundance, had higher recruitment rates with stronger top-down and bottom-up forces. These high productivity regions may be analogous to those found in the Clyde.

Although regional differences were observed in barnacle and macroalgae cover, the main factors contributing to differences in community structure were the position in the loch and height up the shore. New Zealand and Oregon were found to have similar up-shore species distribution patterns with each other which were characterised by degrees of wave exposure (Menge *et al.* 1994; Menge *et al.* 1999). At wave-exposed sites the

upper shores were dominated by barnacles and the lower by algae, sessile invertebrates, and bare space with mussels found between these two regions. At wave-sheltered sites, there was a decrease in mussel abundance with an increase in the abundance of macroalgae. Higher growth rates on exposed shores provide a mechanism which can explain the shift in dominance between filter-feeders on exposed shores and algae on sheltered shores recorded for the South African coast (McQuaid and Lindsay 2000). This corroborated the findings of this study of differences in species abundance at inner and mouth loch positions. The interpretation of the results was quite complex, *M. edulis* and *N. lapillus* were both found to be more abundant at the mouth of lochs with barnacles, macroalgae, *P. vulgata*, and *L. littorea* found to be more abundant at inner loch sites. This was not surprising with the grazers, *P. vulgata* and *L. littorea*, associated with the macroalgae and the predator, *N. lapillus*, associated with its prey, *M. edulis*. Although all sites in this study were matched for similarity in wave exposure, it would be expected that those sites at the mouth of all four lochs would be more prone to an increase in wave exposure compared to those at inner loch sites which would be more sheltered due to the proximity of the east facing shoreline. This was in fact the case with the trend of inner loch sites found to be slightly lower wave exposure of 2.8 to 2.9 $km.kt^2 s^{-2}$ than those sites at the mouth of lochs which had a wave exposure range of 2.9 to 3.2 $km.kt^2 s^{-2}$ (see Chapter 5 for a complete analysis). A change in the rate of water flow would be expected between mouth and inner sites with a greater flow rate found at the mouth of lochs. An increased water flow directly enhances barnacle recruitment and feeding (Sanford *et al.* 1994).

Mytilus edulis, *P. vulgata*, *N. lapillus*, and all Littorinids were found to be more dominant on lower shores although *L. littorea* did favour upper sites on the west coast. Lower shores were also favoured by *S. balanoides* in the Clyde but on the west coast

this species was more abundant at upper heights. Overall the barnacle species were found to have an increased cover at upper sites but this result was probably influenced by species ranges with no Chthamalids or *E. modestus* found at lower shore heights. Similar findings were recorded in Portugal with upper shore levels having a lower species diversity with a higher dominance (Boaventura *et al.* 2002b). It should also be noted that although no significant differences were found between MHWN and MLWN in cover of macroalgae there was a definite increased cover found below the study quadrats at MLWN, especially on the west coast (personal observation). The inner sites of both Loch Melfort and Caolisport were dominated by macroalgae, while the monitoring quadrats on the lower shore of the latter site were overgrown by *Fucus* and lost. It was unclear whether the increase in *Fucus* cover was a result of clearing areas but previous studies have found that re-colonisation of disturbed areas by fucoid species was very slow (Jenkins *et al.* 1999a). No macroalgae were recorded at the lower shore at the mouth of Loch Fyne but they were found to dominate the inner site below MLWN.

2.4.2 Interspecific interactions and species re-colonisation after disturbance

All species under study were found to re-colonise within two months of the initial disturbance event although significant differences in re-colonisation times ranged from less than two months (barnacles and mussels) to two years (*P. vulgata*). The slow rate of *P. vulgata* re-colonisation was, to some extent, unexpected as previous work has shown that the local density of *Patella* increased with the removal of sessile organisms due to the species requirement of cleared substratum for adhesion and grazing (Benedetti-Cecchi *et al.* 1999). The significant recruitment of barnacles within the first two months led to a reduction in cleared substratum which would explain the slow re-

colonisation of *P. vulgata* in this study. The season during which an area is disturbed, as well as the size of the disturbance, has been shown to have a significant impact on the final community structure (Sousa 1984; Petraitis and Latham 1999). Small clearings have a tendency to return to their original state after an initial moderate variation due to differences in initial colonisation events which decline over time but large clearings are more likely to change to an alternative state (e.g. the removal of *Ascophyllum* leading to a site dominated by barnacle-mussel beds) which may be driven by large numbers of recruits with an initial moderate variation as seen in small clearings (Petraitis and Latham 1999; Petraitis and Dudgeon 2005). The change to an alternative state was seen at the upper shore of the mouth of Loch Long which had an initial high mussel cover before clearing with barnacles dominating cleared areas five months from the disturbance and persisting through to the end of the study. A two year study may be insufficient in examining communities when they have changed to an alternative state as they may take up to ten years to return to their original state (Southward 1978).

2.4.3 Variation in recruitment of intertidal barnacle species

Barnacle larvae typically have a minimum amount of time, two weeks or more, that they must spend in the water before they are competent to settle (Roughgarden *et al.* 1985). The settlement of *S. balanoides* appeared later in the Clyde (mid to late April) compared to that of the west coast (early April) with a heavier initial settlement on the west coast, followed by a significant increase in mortality during 2004 when *S. balanoides* was found to have a greater density in the Clyde. A previous study found a positive linear relationship between average flushing time of a bay and *S. balanoides* settlement rate (Gaines and Bertness 1992) which would imply that the lochs in the Clyde have a faster flushing rate than those on the west coast. The situation is complicated further with

larval concentration and arrival rate influenced by hydrodynamic processes such as surface waves, currents, internal wave and tidal bores (Hawkins and Hartnoll 1982; Shanks 1983, 1986; Gaines and Bertness 1992; Pineda 1994), which can increase food supply causing increased growth rate (Bertness *et al.* 1991) and increased disturbance (Gaines and Roughgarden 1987). An increase in coastal rugosity (i.e. the number of inlets, bays, lochs, or estuaries), in particular bays and estuaries, has been shown to generate substantial regional variation in coastal transport and low correlations of barnacle settlement (Kendall *et al.* 1982; Gaines and Bertness 1992). A small tidal range has been shown to play a significant role in reducing the adult stocks of *S. balanoides* to a point where there is difficulty in producing sufficient larvae for more abundant settlement (Crisp and Southward 1958). Loch Caolisport had the smallest tidal range with equal heights at MHWN and MLWN which may partly explain the density shift from the west coast to the Clyde, an area with a greater tidal range which would tend to an increased survival rate of the adult population, after the first year. A reduction in the adult population would not necessarily lead to a reduction in settlement in that area as barnacle populations are considered to be open. The settlement period of *S. balanoides* was found to occur between early winter and spring and ranged between locations from 30 days in Sweden to 71 days on the Isle of Man (Jenkins *et al.* 2000). Low temporal frequency of sampling meant it was not possible to determine the exact settlement time in this study but density peaks were observed during the same months as found by previous studies at Millport (Connell 1961b; Barnes and Powell 1968).

Semibalanus balanoides was the dominant intertidal barnacle throughout the study area. Competition between *S. balanoides* and *Chthamalus* species is well documented (Barnes 1956) with *S. balanoides* able to overgrow an established population of *Chthamalus* within two months (Connell 1961b). Both *Chthamalus* species were found

at higher densities on the west coast where the density of *S. balanoides* was found to be less than that in the Clyde. The estimated settlement time of *C. montagui* was in the autumn between August and November. This corresponded with findings at Millport which showed settlement in September and October, continuing through to December (Connell 1961b) and in SW Ireland where *C. montagui* and *C. stellatus* were both found to settle between early August and October (Delany *et al.* 2003).

2.4.4 Mortality rates of *S. balanoides* and *C. montagui*

High *S. balanoides* mortalities (86 to 96% per year) were noted throughout the region after each settlement period but the population of *C. montagui* was found to be very stable over time. The use of space by *S. balanoides* was not found to be affected by predation or interspecific competition (Rangeley and Thomas 1988) particularly in the high intertidal where wave exposure, desiccation, and intraspecific competition were found to be the major processes affecting abundance and size distributions (Menge 1976). Intraspecific competition could be one explanation for the high *S. balanoides* mortalities at upper shore levels with initial densities as high as 21 individuals/cm^2. Intense predation by *N. lapillus* was found to be the main factor affecting barnacles of the lower shore (Menge 1976) but although the preliminary survey showed *Nucella* was abundant throughout the study area it was not possible, from these data, to accurately determine the abundance of this species at the lower shore. Interspecific competition with fucoids, such as *Ascophyllum*, can also have negative impacts on barnacle settlement (Jenkins *et al.* 1999c; Benedetti-Cecchi *et al.* 2000) with more macroalgae found at lower shores. The stability of the *C. montagui* population was probably due to the higher position of the population on the shore as previous work has shown that this

species has an increased mortality rate at the mid-shore level (Burrows 1988; Delany *et al.* 2003).

2.4.5 Differences in growth rates of *S. balanoides* and *Chthamalus* species

Growth rates were calculated for *S. balanoides*, *C. montagui*, and *C. stellatus* although the latter was only calculated for the mouth of Loch Caolisport. Many studies have been carried out on barnacle growth (see Crisp and Bourget 1985 for an overview) especially *S. balanoides* (e.g. Crisp 1960; Barnes and Powell 1968; Rangeley and Thomas 1988; Bertness *et al.* 1991; Jenkins *et al.* 2001) and only one known study has examined the growth rates of *C. montagui* (Burrows 1988).

Semibalanus balanoides was found to have a growth rate ranging from 0.04 to 0.14 mm/month, reaching a maximum length of between 4.7 and 5.1 mm. Previous studies examining individual growth rates of S. *balanoides* measured the total length of the barnacle rather than the operculum length and substantially the values ranged from 0.34 to 4.80 mm/month (Crisp 1960; for review see Crisp and Bourget 1985; Brind'Amour *et al.* 2002). These growth rates corresponded with a greater mean length after 12 months ranging from 2.5 to 17.5 mm (for review see Crisp 1960). Breaking down the mean length range into height and experiment type (i.e. whether the population was natural or manipulated), natural populations showed a much reduced range of 2.5 to 6 mm (Crisp 1960) which corresponded to the present study although the estimated growth rates were still high at 0.99 mm/month. Individual growth in barnacles has been found to be highly variable (Crisp 1960; Wethey 1983; Dye 1992) and dependent on exposure (Bertness *et al.* 1991) and cover of an algal canopy (Menge 1978) with barnacles found to have slower growth rates at exposed sites or at lower shores with no algal canopy

cover. Slower growth rates have been recorded for barnacles in high population densities (Wethey 1983). This would not explain the reduced growth found in this study since sites in the Clyde, which had a greater growth rate, had a reduced macroalgae cover compared to those on the west coast. Although no significant difference was seen between regions, there was a general trend of the highest (Loch Long) growth rates recorded in the Clyde, an area of high pelagic primary production, and the lowest (Loch Melfort) on the west coast. Similar results were found in New Zealand, Oregon, and Rhode Island (Bertness *et al.* 1991; Menge *et al.* 1999; Menge 2000; Sanford and Menge 2001; Menge 2003) with increased growth rates found at sites of increased productivity. The initial growth phase of the 2003 settlement from May to August of that year showed a similar rate of increase for all lochs in the Clyde, a similar pattern was noted at west coast lochs although it was not as defined (Figure 2.19 to Figure 2.22). Reduced growth rates were recorded during winter months corresponding with findings from previous studies (Barnes and Powell 1968).

Chthamalus montagui were found to have considerably slower growth rates to those measured for *S. balanoides* with the fastest growth rates of *C. montagui* similar to the slowest growth rates of *S. balanoides*. Growth rates of *C. montagui* were found to be slower than those reported for the south of England (Burrows 1988). Seasonal patterns were noted for this species at high shore heights in the south of England with a reduction in growth during winter which was compensated with a growth increase during summer months (Burrows 1988). No seasonal pattern was noted for the 2003 settlement in this study but the 2004 settlement did show a reduction in the growth rate between September 2004 and March 2005 (Figure 2.29). Initial growth rates were found to be similar for both *C. montagui* and *C. stellatus* (Burrows 1988) which, prior to 1976, were classed as one species, *C. stellatus* (Southward 1976). Few data were

available on growth rates of *C. stellatus* (present study) with the exception of the established population at the mouth of Loch Caolisport (Figure 2.30). Little growth was seen in this population during the 27 months of study but growth did decrease during the winter months of the first year although no decrease in growth rate was noted during the winter months of the second year. The lack of growth during winter months was observed during the first winter for *C. stellatus* (although this species was most probably *C. montagui*) at Millport with animals reaching 3 to 4.5 mm after 12 months from settlement with a slower second year of growth to a mean length of 6 to 7 mm (Barnes 1956). These findings were considerably higher than those found in this study for *C. montagui* which recorded a maximum individual length of 3.6 mm from the 2003 settlement after one year of growth and 3.7 mm in the established population of *C. stellatus*. The large barnacle lengths observed by Barnes (1956) may be due to the experimental conditions of constant submergence and clearing of other species to reduce competition for space.

2.4.6 Summary

The aim of this study was to test the effect of pelagic primary production, over a large scale, on the structure of intertidal communities in western Scotland. It was predicted that significant regional differences would be found between the filter feeder dominated Clyde and the macroalgal dominated west coast. To an extent, this prediction was correct with more macroalgae found on the west coast and the Clyde dominated by barnacles with *S. balanoides* found to be significantly larger within the latter region. However, the more dominant significant effect was on a much smaller scale of within loch variation suggesting site-specific effects had a greater role in structuring the intertidal community within these regions.

Oceanographic processes acting on a large scale between regions directly affect barnacle recruitment (Table 2.1) but once recruited into the population, site-specific influences, such as wave exposure and the rate of water flow, have a more significant impact in structuring the community. Barnacle feeding rates increase with an increase in water flow (Sanford *et al.* 1994) which would consequently cause an increase in barnacle size. The combination of an increased size at high flow sites and an increased number of settled barnacles in the Clyde, would lead to propagation up the food chain which would affect the size and distribution of *N. lapillus*. Site-specific effects acted on all *S. balanoides* cohorts while regional effects acted on the adult population. The latter would most probably affect longevity of the barnacles while the site-specific affects growth rates.

Chapter 3 Growth rates of intertidal molluscs in areas of contrasting pelagic primary production: a multi-technique analysis

3.1 Introduction

Estimation of species growth rates has been well documented throughout the intertidal community and plays an integral part in understanding the structure of that ecosystem. Growth rate, or secondary production, is a good reflection of food availability and thus an indicator of energy flow in a system. Measuring growth can be highly taxon-dependent with different techniques employed for animals depending on the biology such as the presence of an outer shell, and life history of the animal under study. An outer shell provides a convenient attachment site for labelling and tagging which minimises the stress to the animal compared with more invasive techniques, while understanding the life history of the animal will determine whether the movements of the animal could be artificially restricted or if it would be detrimental to remove or handle the animal.

Preliminary surveys of species abundances (see section 2.3.1) found only six animal species in the top 20 most abundant flora and fauna throughout both regions. These species were *Semibalanus balanoides* (L., 1767), *Patella vulgata* (L., 1758), *Nucella lapillus* (L., 1758), *Littorina littorea* (L., 1758), *Mytilus edulis* (L., 1758), and *Chthamalus montagui* Southward, 1976 which were ranked in order of most abundant as one, four, nine, 12, 13, and 14 respectively. Measurements of population growth rates were carried out on *S. balanoides* (section 2.3.4) and *C. montagui* (section 2.3.6) with the growth rates of the remaining four species still to be determined.

Free swimming larvae are found in *L. littorea* (Fish 1972; Kemp and Bertness 1984; Yamada 1987), *P. vulgata* (Lewis and Bowman 1975), and *M. edulis* (Bayne 1964; Page and Ricard 1990) with *N. lapillus* the only species regarded as having a closed

population (Connell 1970; Spight 1974; Spight and Emlen 1976). The lack of a dispersal stage causes adult *Nucella* to have a small lifetime range (Etter 1996).

Ideally a non-destructive, *in situ* experiment examining growth over time would be used and, if possible, relating the change in growth with age (as discussed by Francis 1988). Tagging the animal either by engraving the shell (Dolmer 1998), paint/ink labelling (Page and Hubbard 1987; Dolmer 1998), or shellfish tags (Millstein and O'Clair 2001; Honkoop *et al.* 2003) are common methods used when investigating growth over time and are frequently combined with cages (Theissen 1975; Kautsky 1982; Palmer 1983; Page and Hubbard 1987; Honkoop *et al.* 2003) or fenced off areas which restrict movements (Boaventura *et al.* 2002a). Restricting animal movements poses inherent problems which may affect their growth over prolonged periods by limiting their foraging range. This would not apply to sessile animals such as barnacles and mussels with previous work showing that caging mussels had no effect on their growth (Leonard *et al.* 1998). However, long-term marking of mussels (e.g. surface filing, growth edge notching) typically results in physical disturbance to individuals that may lead to shell deformations and/or uncharacteristic growth rates (Kaehler and McQuaid 1999). Growth studies carried out on mussels (Seed 1968; Bayne and Worrall 1980; Stirling and Okumus 1994; Buschbaum and Saier 2001; Mills and Côté 2003; Waite *et al.* 2005) and limpets (Tablado *et al.* 1994; Thompson *et al.* 2000; Jenkins and Hartnoll 2001; Boaventura *et al.* 2002a; Dunmore and Schiel 2003) were based on changes in shell morphology, particularly shell length whereas the intertidal molluscs, *N. lapillus* and *L. littorea*, have been known to show negative shell length changes due to erosion of the shell lip (Palmer 1982). In this instance, change in body mass was estimated through measurement of weight in air and water using conversion equations to determine growth (Palmer 1982; Burrows and Hughes 1990).

Transplantation experiments are often used when examining growth rates between two contrasting regions in order to rule out any genotype or phenotype differences between regions. Mussels are ideal for this type of experiment as they are easily re-located and it is possible to keep them caged, reducing the number of animals lost, while not hindering feeding. A basic transplant experiment would involve transplanting mussels from a site of high pelagic primary production to a site of low pelagic primary production and vice versa. The growth rates of the mussels which were moved would be expected to match those of the mussels already at that site. However, this type of experiment requires that the act of moving and disturbing mussels be controlled. To control for movement, mussels should be translocated from a site of high pelagic primary production to another site of high pelagic primary production and similarly with mussels found at low pelagic primary production sites. Disturbance should be controlled for by carrying out identical procedures to the transplantations and translocations, but re-positioning the mussels at the site of origin (see Honkoop *et al.* 2003 for an in-depth description of the technique).

Relating growth rate to age is not always possible since this needs a reliable method for determining the age of the animal (Francis 1988). Annual growth rings in mussels have been well documented (Theissen 1975; Seed 1976; Hunt and Scheibling 1995; Stoica *et al.* 2000; Gilek *et al.* 2001; Millstein and O'Clair 2001) with the formation caused by periods of suspended growth. In temperate areas, rings are most likely formed annually where shell growth is greatly decreased or suspended in winter due to low temperatures (Seed 1976). The number of external growth rings on the shells of mussels found in tide pools in Nova Scotia, Canada, was exponentially related to shell length assuming an annual deposition of rings (Hunt and Scheibling 1995). Growth rings have also been observed in mussels picked from rivers or lakes (Stoica *et al.* 2000; Gilek *et al.* 2001;

Millstein and O'Clair 2001). However, not all *Mytilus* populations show such periodicity in ring formation (Seed 1976).

Many studies have been carried out examining rates of growth in intertidal organisms with growth found to vary according to size, age, genotype (Diehl and Koehn 1985), physical disturbance (Harger 1970), and density (Seed 1968; Kautsky 1982; Jenkins and Hartnoll 2001). These factors have consequently been linked with environmental parameters such as temperature (Lewis *et al.* 1982; Etter 1989), salinity (Dolmer 1998; Westerbom *et al.* 2002), water movement (Griffiths 1980a, 1980b; Sebens 1984; Van Erkom Schurink and Griffiths 1993; Camacho *et al.* 1995; Dolmer 1998; Leonard *et al.* 1998; McQuaid and Lindsay 2000), and concentration and quality of the food consumed (Seed 1976; Griffiths 1980a, 1980b; Tsuchiya 1980; Palmer 1983; Moran *et al.* 1984; Burrows and Hughes 1990; Page and Ricard 1990; McQuaid and Lindsay 2000; Menge *et al.* 2002). The response of growth to most of these environmental factors is non-linear (Archambault *et al.* 1999) and species specific (Thomas 1986; Leonard *et al.* 1998). The aim of this chapter was to determine the growth rates of the predator, *N. lapillus*, the grazers, *L. littorea* and *P. vulgata*, and the filter feeder, *M. edulis*, and whether differences in growth rates were related to regions (Clyde and west coast) of contrasting pelagic primary productivity. In order to investigate changes in growth rates the following null hypothesis was stipulated:

H_0 = No difference in individual growth rate over time will be observed between areas of high (Clyde) and low (west coast) pelagic primary productivity in *N. lapillus*, *L. littorea*, *P. vulgata*, and *M. edulis*.

In order to test the null hypothesis different techniques were used which were dependent on the species being tested. A mark-recapture technique was used for both *N. lapillus* and *L. littorea* but instead of measuring change in shell length, which has been shown to have inherent drawbacks as discussed previously, change in flesh weight, which is considered to be a more accurate measure, was used. In order to minimise stress, images from Chapter 2 were used, in conjunction with an image analysis package, to measure changes in shell length of *P. vulgata* while a transplant technique (see earlier discussion of this section) was used for *M. edulis*.

An area of high pelagic primary productivity, the Clyde, would have an increased quantity of food for filter feeding organisms such as barnacles and mussels. It would be expected that the increase in food availability would lead to a corresponding increase of growth in the mussel, *M. edulis*, compared with a lower growth rate on the west coast. The increased food supply, number of filter feeders, in the Clyde would be expected to benefit *N. lapillus*, which preys on both mussels and barnacles, by having an increased growth rate within this area. Littorinids and *P. vulgata* depend on macroalgae and microalgae for growth. It has been shown previously (Chapter 2) that the west coast has significantly more macroalgae than the Clyde and although macroalgal abundance is not directly related to pelagic primary production, it would be expected that the growth rates of both *L. littorea* and *P. vulgata* would be greater on the west coast compared to the Clyde. The increased abundance of barnacles in the Clyde would hinder foraging time and efficiency of *P. vulgata* and so also contribute to a lower growth rate of this species in the Clyde.

3.2 Materials and Methods

Growth rates of *Nucella lapillus*, *Littorina littorea*, *Patella vulgata*, and *Mytilus edulis* were measured at the eight sites previously described in Chapter 2 (for details of site locations see Figure 2.1). Three techniques were employed and these are described separately in the following sections; mark-recapture (*N. lapillus* and *L. littorea*), photographic analysis (*P. vulgata*), and transplantation (*M. edulis*).

3.2.1 Estimation of growth rates in gastropods using mark-recapture methods

At each site, 50 animals of each species (*N. lapillus* and *L. littorea*) were collected in May 2004, placed in a labelled mesh bag and taken back to the laboratory for marking, weighing, and measuring. A white number printed on a red background was affixed onto the dry, and roughened, shell of each animal with epoxy adhesive (Araldite® Rapid). Once dry, each animal was measured (shell length, aperture length, and aperture thickness, Figure 3.1), weighed dry in air and weighed suspended in seawater to determine flesh weight as carried out by Palmer (1982) and later used by Burrows and Hughes (1990). Stage of maturity (juvenile or adult) was also scored for all *Nucella*. The presence of aperture teeth and a thickening of the aperture lip have been shown to be indicators of *Nucella* maturity (see Burrows and Hughes 1990). *Littorina littorea* were found to mature at a shell length greater than 19 mm (Sharp 1998). After tagging and measurements, all animals were released at the collection sites and in August 2004, April 2005, and July 2005 each site was re-visited and searched (an hour per site) for marked animals. Recaptured animals were returned to the laboratory, weighed and measured, as previously described, and subsequently released at their

original location. All animals were kept in the aquaria under constant conditions for no more than one week while at the laboratory.

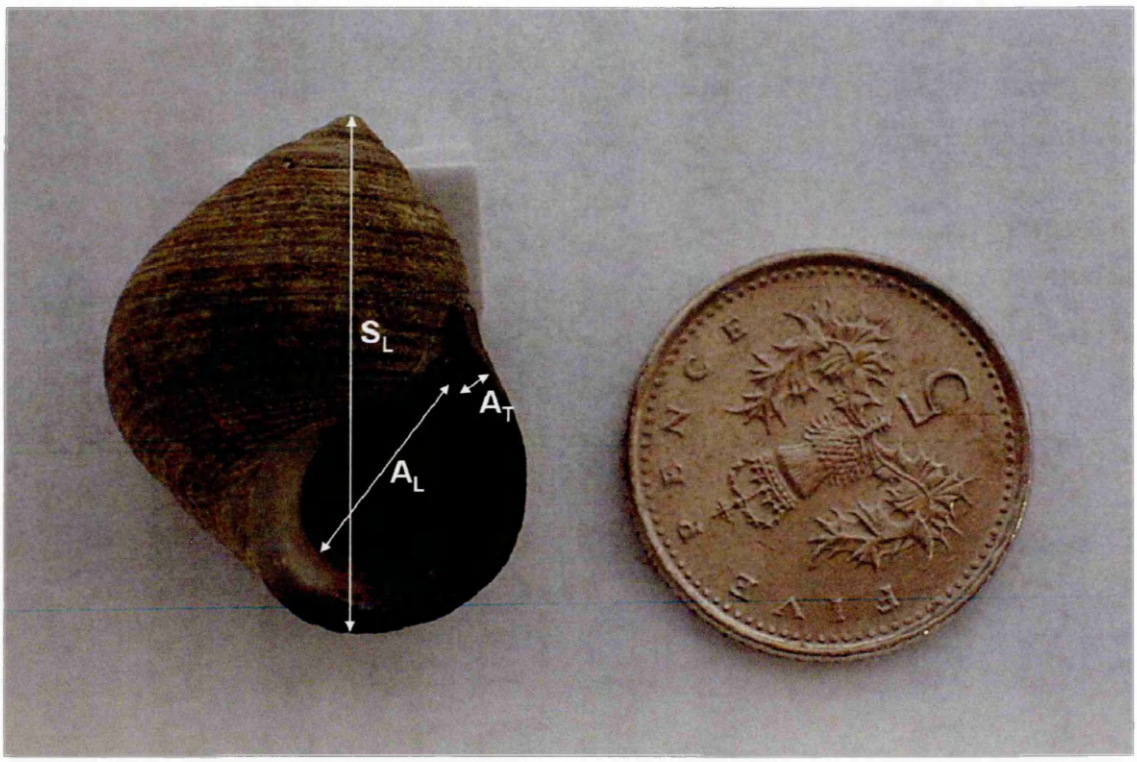


Figure 3.1 Shell length (S_L), aperture length (A_L), and aperture thickness (A_T) were measured for both *L. littorea* (shown in picture) and *N. lapillus*. The coin is 18.0 mm in diameter.

3.2.2 Estimation of shell and body weight in live mark-recaptured animals

Animals were left to dry in air for 24 hours and, before weighing in air, the aperture was dabbed dry with a paper towel to ensure as little water as possible was left within the mantle cavity. Before weighing animals in sea water, they were kept submerged in an aquarium tank for 24 hours to ensure as little air as possible was left within the mantle cavity. Immersed weight of the whole body was obtained by carefully placing the animal in a purpose built cradle which was suspended below a balance using fine

fishing wire. The cradle was immersed in a beaker of seawater and each animal was weighed individually. Seawater has a density close to that of the snails internal tissue (Palmer 1982; Burrows and Hughes 1990) and hence this technique of immersed weight gives an estimation of the weight of the shell. Combining this information with weighing the whole animal in air (dabbed dry with paper towels) and adding a correction (see section 3.2.3) it is possible to obtain a non-destructive estimation of the dry weight of the flesh.

3.2.3 Calibration of shell and body mass estimation techniques of Palmer (1982)

To avoid interference with the ongoing experiment, *N. lapillus* (n = 25) and *L. littorea* (n = 25) were collected from the inner site at Loch Melfort. These animals were taken back to the laboratory, weighed, and measured as described previously. The shell of each air dried animal was carefully broken, the flesh removed, and dabbed dry with a paper towel. All shell fragments and flesh of each animal were weighed in air and then dried at 60°C to a constant weight. Regressions were then obtained between shell dry weight and immersed whole body weight, and for dab-dried flesh weight and dry flesh weight for both species (Table 3.1). The regression of shell dry weight from immersed whole body weight (regressions 1 and 2 of Table 3.1) was used to estimate actual shell weight from immersed weight of the whole animal. Thus, the dabbed dry flesh weight of the animal will be equal to the weight of the animal in air minus the estimated shell mass from this regression (equations 5 and 6 of Table 3.2). By incorporating into this equation the second regression (regressions 3 and 4 of Table 3.1), it is possible to obtain an equation that gives an estimated flesh dry weight from immersed whole body weight, and weight in air (equations 7 and 8 of Table 3.2).

Table 3.1 Regressions of dried shell weights from immersed whole body weights and dabbed dry flesh weights from dried flesh weights for both *N. lapillus* and *L. littorea*. Weights were measured in grams with the number of individuals (n) shown for each regression equation with the corresponding R^2 value.

Regression number	Species	n	Regression equation	R^2
Dried shell weight (y) from immersed body weight (x)				
1	*N. lapillus*	25	y = 1.5558x + 0.0147	0.9994
2	*L. littorea*	25	y = 1.5403x + 0.0324	0.9965
Dabbed dry flesh weights (y) from dried flesh weights (x)				
3	*N. lapillus*	25	y = 2.6524x + 0.0662	0.9532
4	*L. littorea*	25	y = 2.7745x + 0.0997	0.9359

Table 3.2. Equations to determine flesh dry weight (FD) from weight in air (AW), immersed whole body weight (WW), and dab-dried flesh weight (FW) incorporating the regressions from Table 3.1.

Description & equation number	Species	Equation
Subtracting regressions 1 and 2 from weight in air		
5	*N. lapillus*	FW=AW-(1.5558WW+0.0147)
6	*L. littorea*	FW=AW-(1.5403WW+0.0324)
Incorporating in regressions 3 and 4		
7	*N. lapillus*	FD=(AW-1.5558WW-0.0809)/2.6524
8	*L. littorea*	FD=(AW-1.5403WW-0.1321)/2.7745

3.2.4 Measurement of growth of *Patella vulgata* from photographic monitoring quadrats

Permanent 30x30 cm quadrats (see section 2.2.2) which were set up for the colonisation and community structure experiment were used to measure shell total lengths of *Patella vulgata*. A PC program (see section 2.2.4) was used in the same way as that to measure barnacles, with the exception that lengths of specific individual *Patella* were measured over time rather than different sub-samples of the population in each image on each sampling occasion. It was possible to identify each limpet by its shell markings and the barnacles which were growing on the shells (Figure 3.2).

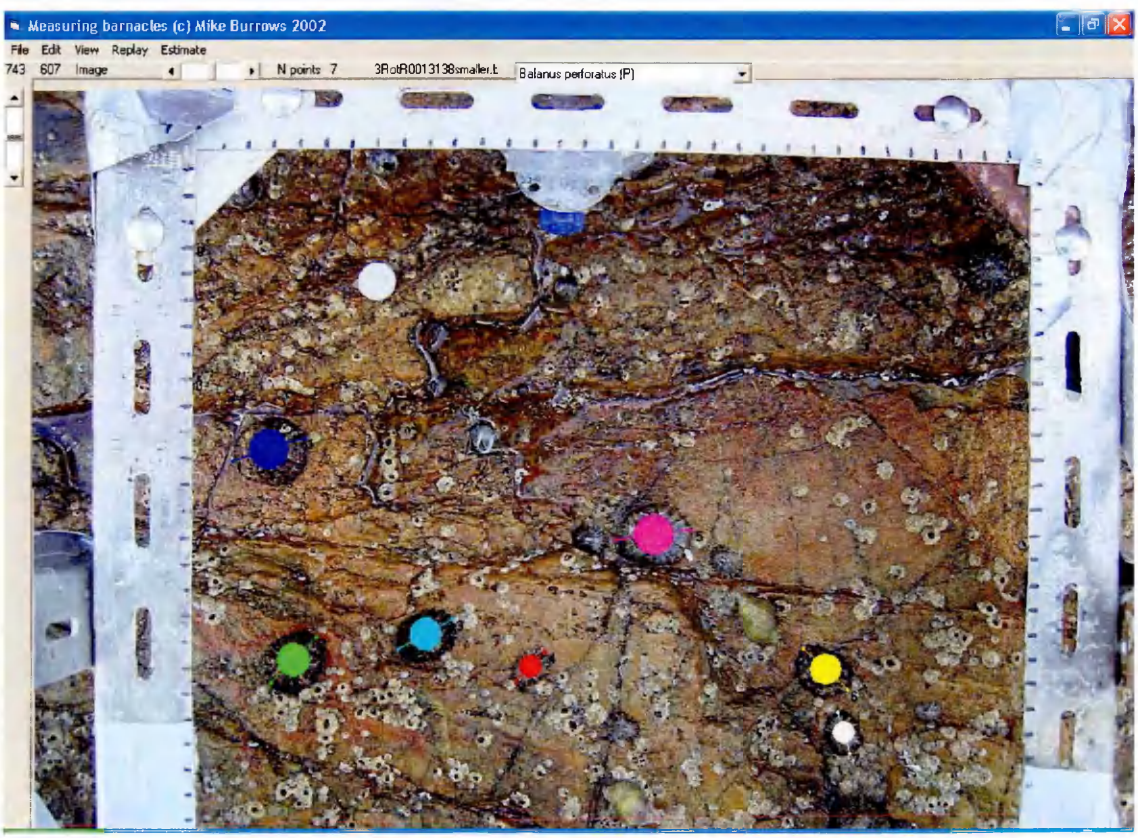


Figure 3.2. Measuring limpet growth using an image analysis package designed for barnacles. In this case, colours do not denote species but rather individuals.

3.2.5 Measuring growth of *Mytilus edulis* using a transplantation experimental design

Two contrasting lochs were chosen to study *M. edulis* growth in a transplant experiment. The lochs chosen were Loch Long in the Clyde system (high pelagic primary production) and Loch Caolisport on the west coast (low pelagic primary production). Mussels were sampled from the inner sites of both lochs following the experimental design of Honkoop *et al.* (2003) (see below and Figure 3.3). The treatments were:

1. Mussels transplanted from Long inner to Caolisport inner (L-C).
2. Mussels translocated from Long inner to Long mouth (Linn-Lmou).
3. Disturbed mussels at Long inner (L-L).
4. Mussels transplanted from Caolisport inner to Long inner (C-L).
5. Mussels translocated from Caolisport inner to Caolisport mouth (Cinn-Cmou).
6. Disturbed mussels at Caolisport inner (C-C).

The purpose of the experiment was to determine if there were differences in mussel growth between two lochs (Caolisport and Long) which can be calculated from treatments three and six. The remaining treatments act as controls to test differences between lochs (treatments 1 and 4) and within lochs (treatments 2 and 5). An additional control of undisturbed mussels may also be incorporated, as suggested by Honkoop *et al.* (2003), although this poses problems in itself. Undisturbed mussels would have to be measured and marked *in situ* which would not be practical at a site with high mussel abundance. Since mussels for all treatments were caged throughout the experiment, additional controls would have to be set up to incorporate any cage artifacts.

Ideally, the above treatments would be applied to all eight sites under study but this was not possible with the lack of large quantities of mussels at most sites and the logistics of carrying out such sampling on such a large spatial scale. Due to the small number of mussels found at the inner sampling site of Loch Caolisport (see Chapter 2) it was decided to set this experiment up at a nearby site, St Columba's Cave (Caolisport upper) with an abundant mussel population (Appendix 2.1).

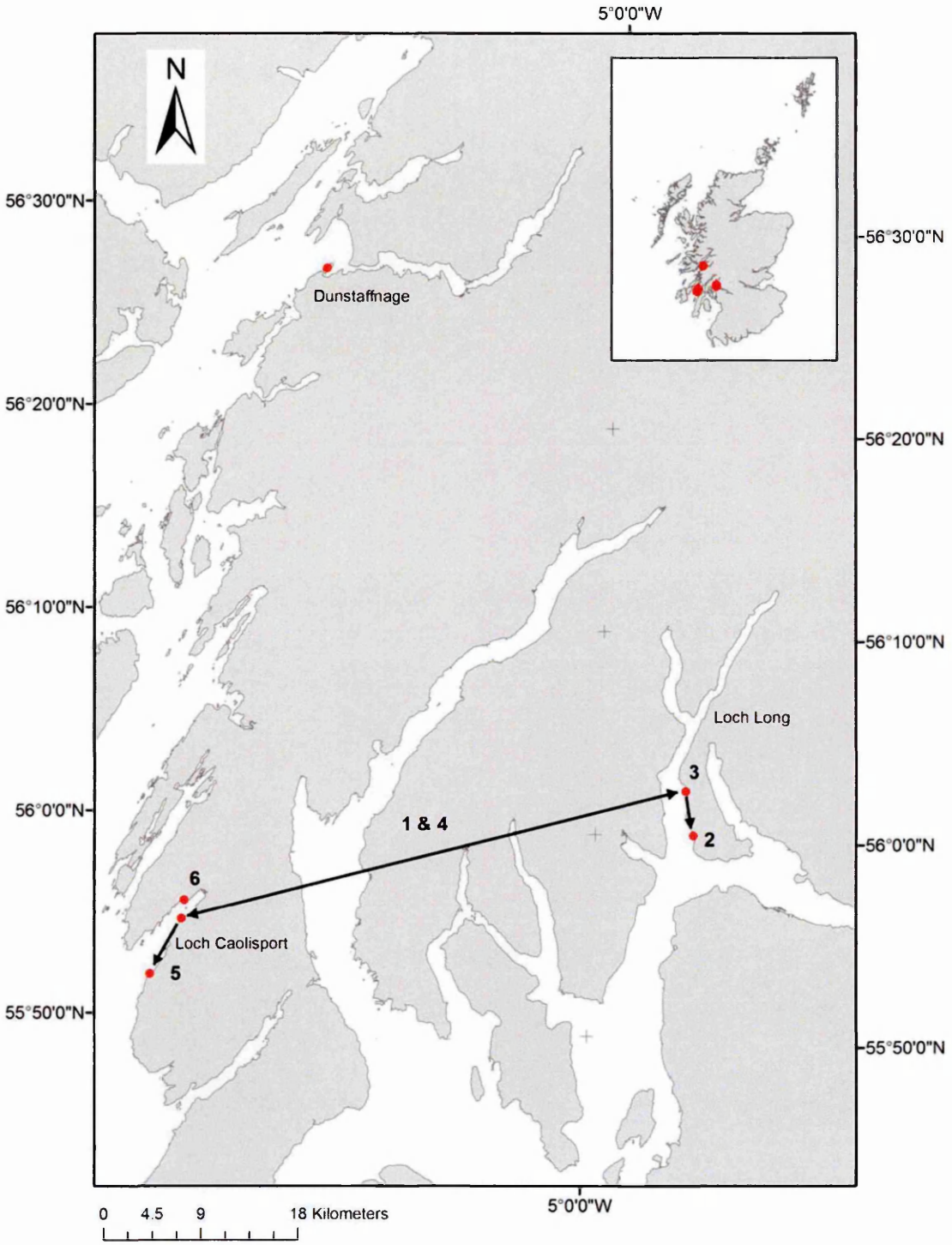


Figure 3.3. Locations of sites used to transplant (treatments 1 and 4), translocate (treatments 2 and 5), and disturb (treatments 3 and 6) mussels between and within Lochs Caolisport and Long.

Mussels were carefully removed from the inner sites of each loch with a paint scraper in April 2004 and an etch mark sawn onto the shell tip with a hacksaw. Care was taken not to saw too deep and break the seal of the shell. Ten mussels (size range 15 mm to 57 mm, average 25 mm) were placed into plastic mesh cages which were secured to the bedrock with 8 mm brass screws at mid tide level (MTL). The cages were 120 mm long, 110 mm wide, 30 mm deep, with a 5 mm mesh size and a 30 mm lip along the length (Figure 3.4). A 24V hammer drill was used to drill two 8 mm holes per cage. Each treatment was replicated four times with mussels remaining in the cage for the duration of the experiment. Mussel growth was measured 162 days afterwards by calculating the difference between measurements from the etch to the umbo and from the shell lip to the umbo along the same line using digital calipers (Moore and Wright digital caliper, error ±0.02 mm). Unfortunately the cages at the alternative inner site of Loch Caolisport had been vandalized and so data from the experiment were incomplete.

It was decided to repeat the transplant experiment but to re-locate the alternative inner site at Loch Caolisport to the original sampling site (see Chapter 2). It was also decided to take the collected mussels back to the laboratory for marking using a less invasive technique which ensured more accurate measurements of each mussel. In the laboratory, mussels were cleaned of all fouling material and dried with paper towels. White numbers printed on a red paper background were stuck onto the shell using epoxy adhesive (Araldite® Rapid) and left to dry. Once dry, mussel length, breadth, and depth were measured using digital calipers (Figure 3.5). Mussels were kept in the aquaria, at constant conditions, for no longer than a week before being placed into the cages, as described above, in September 2004. In April and July 2005 all mussels were removed from their cages, taken back to the laboratory, and measured as described previously.

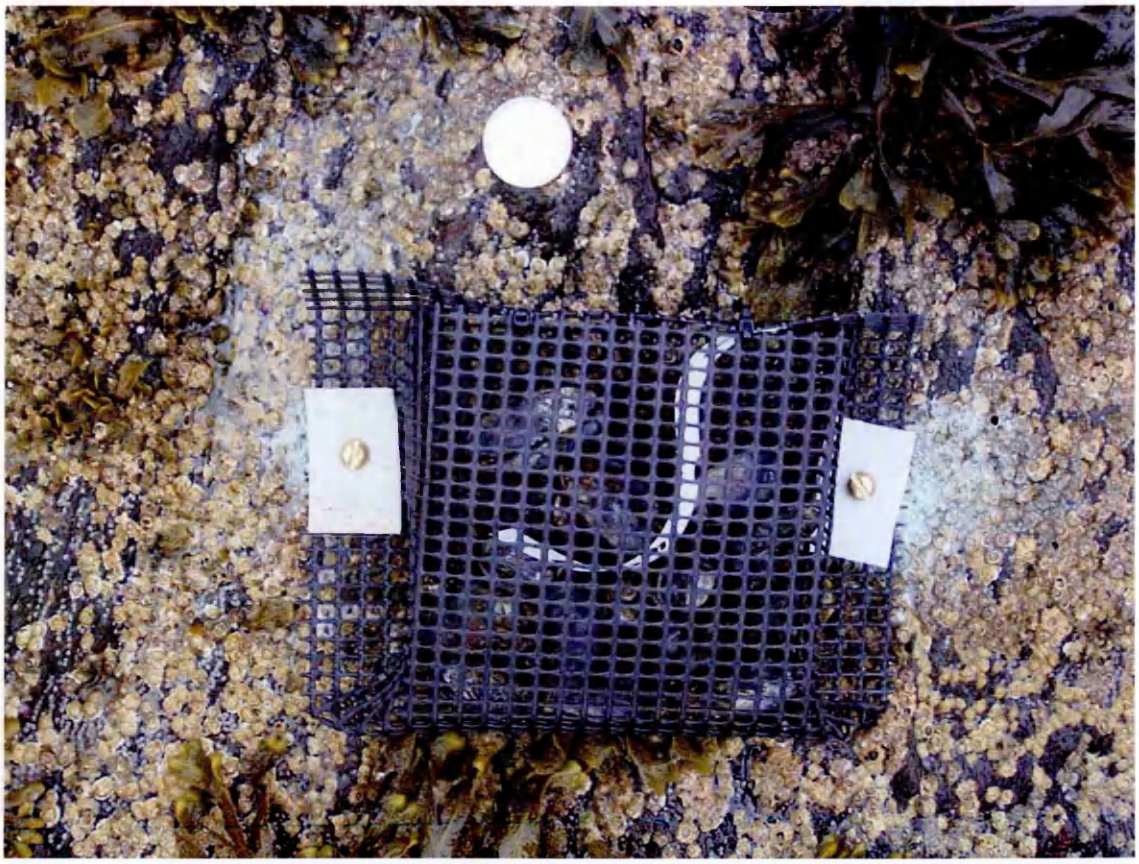
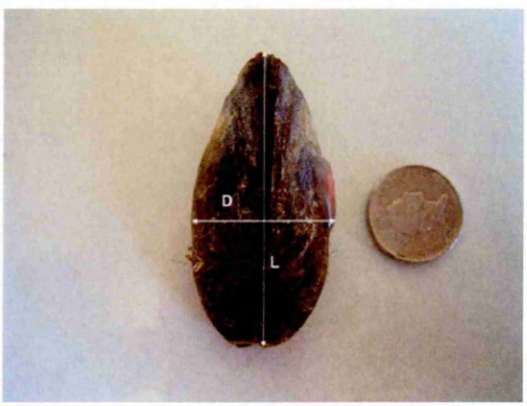


Figure 3.4. An example of a plastic cage used in the mussel transplant experiment. Each cage was labelled and secured to the bedrock with two brass screws and washers. Coin diameter is 18.0 mm.



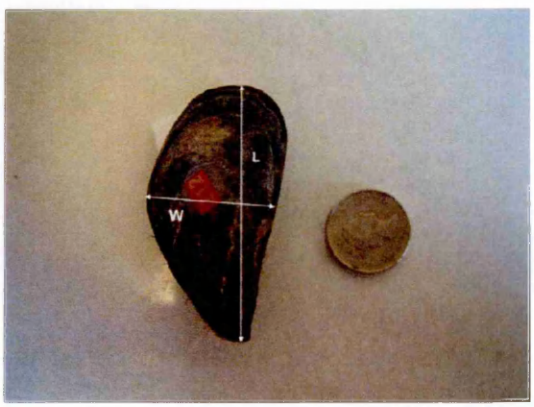


Figure 3.5. Length (L), width (W), and depth (D) measurements which were taken of *M. edulis*. Note the depth measurement includes the label and adhesive to ensure consistency throughout the experiment. Coin diameter is 18.0 mm.

3.3 Results

Analysis of covariance was used to examine the growth rates of *N. lapillus*, *L. littorea*, and *P. vulgata*. Reduced models of the significant results were carried out with the resulting coefficients used to construct a regression for each species. Growth rates of *M. edulis* were analysed with a one-way ANCOVA design.

3.3.1 Growth rates of *N. lapillus* from mark-recapture experiments

More *N. lapillus* were recaptured at west coast sites during the three sampling periods with 40% of the overall recaptures occurring at Loch Melfort (Table 3.3). Due to a decrease in the number of recaptures at 328 days (April 2005) and 441 days (August 2005) from the start of the experiment, only those animals recaptured 91 days (August 2004) from the start (May 2004) were used in the statistical analysis. All weights were converted to estimated flesh dry weight (equation 7 of Table 3.2). Loch Fyne had the lowest initial mean dry weight and Loch Caolisport had the greatest mean dry weight (Figure 3.6). The greatest increase in mean dry weight was recorded at the mouth of Loch Melfort (0.133 g in 328 days) with the equivalent in the Clyde found at the mouth of Loch Long (0.132 g in 441 days). The slowest increase was recorded at the inner site of Loch Caolisport (0.092 g in 441 days).

Table 3.3 Number of *N. lapillus* recaptured after 91, 328, and 441 days from the start of the experiment. Initial sample numbers are shown.

Site	Initial	91 days	328 days	441 days
Fyne mouth	50	3	5	1
Fyne inner	50	5	8	3
Long mouth	50	1	1	5
Long inner	50	5	5	0
Caolisport mouth	50	21	5	1
Caolisport inner	50	4	4	2
Melfort mouth	50	11	2	0
Melfort inner	50	19	13	6

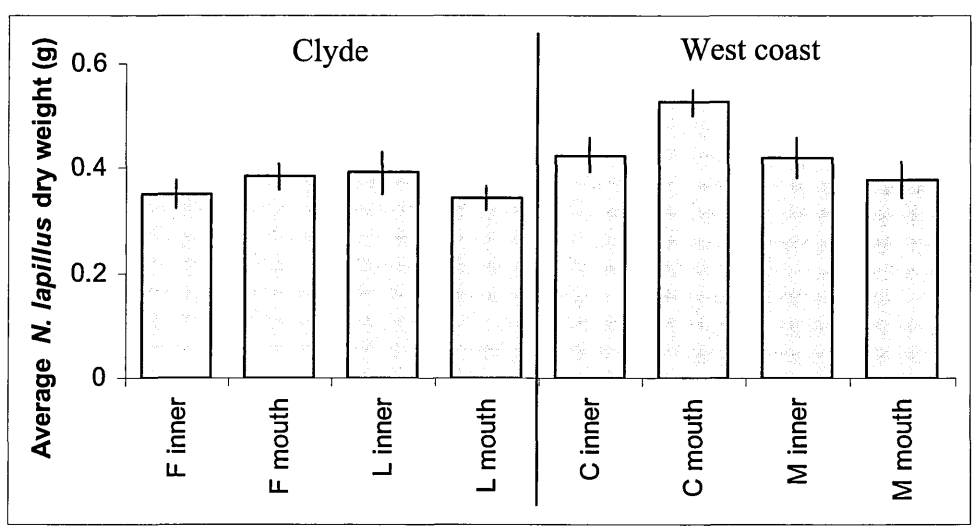


Figure 3.6 Initial mean dry weight of *N. lapillus* at inner and mouth positions of Lochs Fyne (F), Long (L), Caolisport (C), and Melfort (M) in May 2004. Fifty animals were measured at each site. 95% confidence intervals are shown.

Due to the low number of recaptured animals (Table 3.3), it was not possible to carry out a full analysis incorporating a nested ANCOVA design. For this reason, the analysis was carried out on lochs with no regional or positional effects taken into account. A total of 32 juvenile *N. lapillus* were initially measured with 31% being recaptured 91 days later. The change in estimated dry weight of these juvenile animals was found to be significantly larger than the recaptured adults which were found to have a significantly larger initial estimated dry weight than the juveniles (Table 3.4, Figure 3.7, and Figure 3.8). No significant differences were found between the covariate of initial estimated dry weight and loch or maturity (Table 3.4), although highly significant differences were found in the reduced model.

Table 3.4 Results from an analysis of covariance examining differences in slopes of the initial and final length interactions of *N. lapillus* after 91 days of growth.

	d.f.	**SS**	**MS**	**F ratio**	**P value**
Loch	3	0.0031	0.0599	95.98	0.635
Maturity	1	0.0004	0.0212	22.32	0.032
Initial	1	0.0990	0.4878	430.09	<0.001
Loch×Maturity	3	0.0019	0.0010	0.85	0.472
Loch×Initial	3	0.0022	0.0006	0.52	0.667
Maturity×Initial	1	0.0008	0.0002	0.18	0.674
Loch×Maturity×Initial	3	0.0025	0.0008	0.74	0.532
Residual	51	0.0581	0.0011		
Total	66				

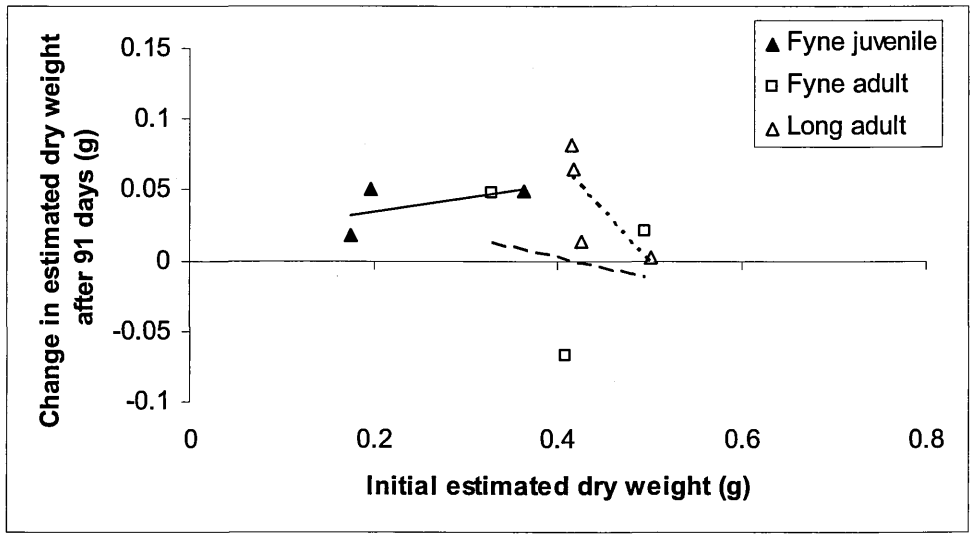


Figure 3.7 Change in estimated dry weight after 91 days for juvenile *N. lapillus* at Loch Fyne (solid line, $y = 0.1003x+0.015$, $R^2 = 0.304$) and adults at Lochs Fyne (large dashed line, $y = -0.144x+0.060$, $R^2 = 0.040$) and Long (small dashed line, $y = -0.6974x+0.348$, $R^2 = 0.559$).

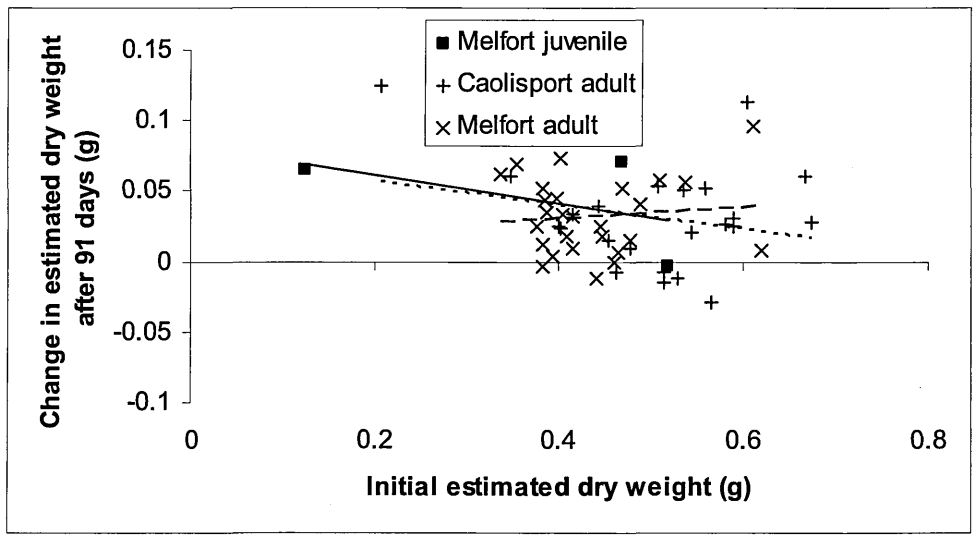


Figure 3.8 Change in estimated dry weight after 91 days for juvenile *N. lapillus* at Loch Melfort (solid line, $y = -0.1041x+0.083$, $R^2 = 0.296$) and adults at Lochs Caolisport (small dashed line, $y = -0.0853x+0.074$, $R^2 = 0.060$) and Melfort (large dashed line, $y = 0.0414x+0.014$, $R^2 = 0.012$).

3.3.2 Growth rates of *L. littorea* from mark-recapture experiments

More *L. littorea* were recaptured at west coast sites with 31% of the overall recaptured animals from Loch Caolisport (Table 3.5). As with *N. lapillus* the number of recaptured *L. littorea* decreased with time and so only those recaptured after 91 days in August 2004 were used in the statistical analysis. No animals were found in August 2005 throughout the Clyde area or during April 2005 in Loch Long. Over the first 91 days the greatest mean increase in dry weight of 0.143 g was found at the inner site of Loch Caolisport with the smallest increase in mean dry weight of 0.025 g found at the mouth of Loch Melfort (Figure 3.9). The greatest increase in the Clyde of 0.120 g was found at the mouth of Loch Long with the inner site of Loch Fyne found to have the smallest increase in mean dry weight in the Clyde of 0.055 g. The site at the mouth of Loch Fyne was the only location where a decrease in mean dry weight was observed.

Table 3.5 Number of *L. littorea* recaptured after 91, 328, and 441 days from the start of the experiment. Initial sample numbers are shown.

Site	Initial	91 days	328 days	441 days
Fyne mouth	45	6	0	0
Fyne inner	50	5	0	0
Long mouth	50	17	2	0
Long inner	50	4	2	0
Caolisport mouth	50	3	2	2
Caolisport inner	50	12	4	1
Melfort mouth	50	3	2	2
Melfort inner	49	6	3	2

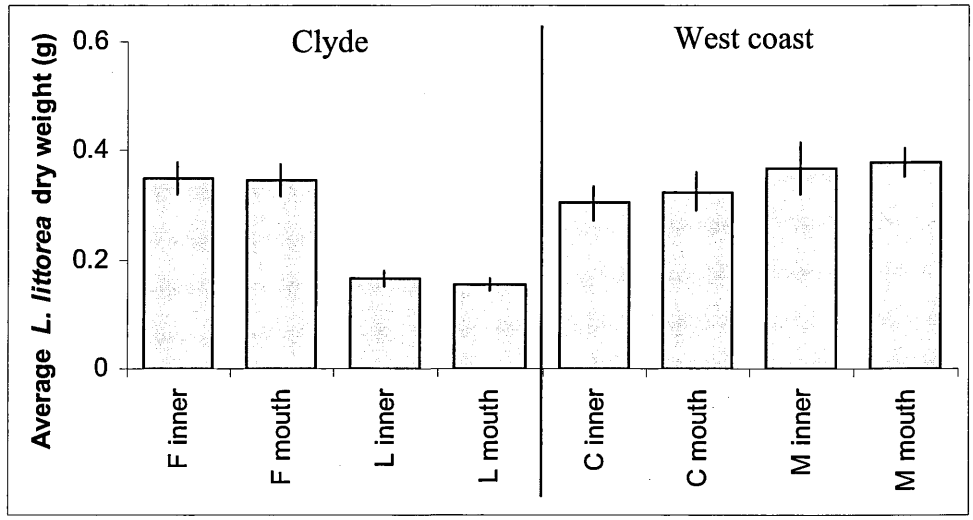


Figure 3.9 Mean initial dry weight of *L. littorea* at inner and mouth positions of Lochs Fyne (F), Long (L), Caolisport (C), and Melfort (M). 95% confidence intervals are shown.

Sharp (1998) noted that *L. littorea* matured at a shell length greater than 19 mm. Maturity was not determined during this study and so, in order to minimise the effect of initial size on growth rates of *L. littorea*, animals were categorised into two groups; small (shell length <21 mm) and large (shell length ≥21 mm). As with *N. lapillus* (section 3.3.1), there was not a sufficient number of recaptured animals at inner and mouth sites to statistically determine whether growth rates varied between loch positions (Table 3.5). Due to this, *L. littorea* were grouped by loch before carrying out an analysis of covariance.

A total of 157 small *L. littorea* were initially sampled with a recapture rate of 3.2% after 91 days. Highly significant differences were found in loch, size, and initial estimated dry weight (Table 3.6, Figure 3.10 and Figure 3.11). Small *L. littorea* were found to have a significantly faster growth rate from a smaller initial estimated dry weight compared with large animals. Animals measured in Loch Long were found to be significantly smaller than Lochs Fyne, Caolisport, and Melfort, with the latter loch found to have the largest measured animals. No significant differences were found between the covariate of initial estimated dry weight and loch or size (Table 3.6), although highly significant differences were found in the reduced model.

Table 3.6 Results from an analysis of covariance examining differences in slopes of the initial and final length interactions of *L. littorea* after 91 days of growth.

	d.f.	**SS**	**MS**	**F ratio**	**P value**
Loch	3	0.0059	0.0700	25.24	<0.001
Size	1	<0.0001	0.0543	19.56	<0.001
Initial	1	0.0127	0.1597	57.55	<0.001
Loch×Initial	3	0.0083	0.0028	0.99	0.405
Size×Initial	1	0.0001	0.0001	0.02	0.883
Residual	42	0.1165	0.0028		
Total	51				

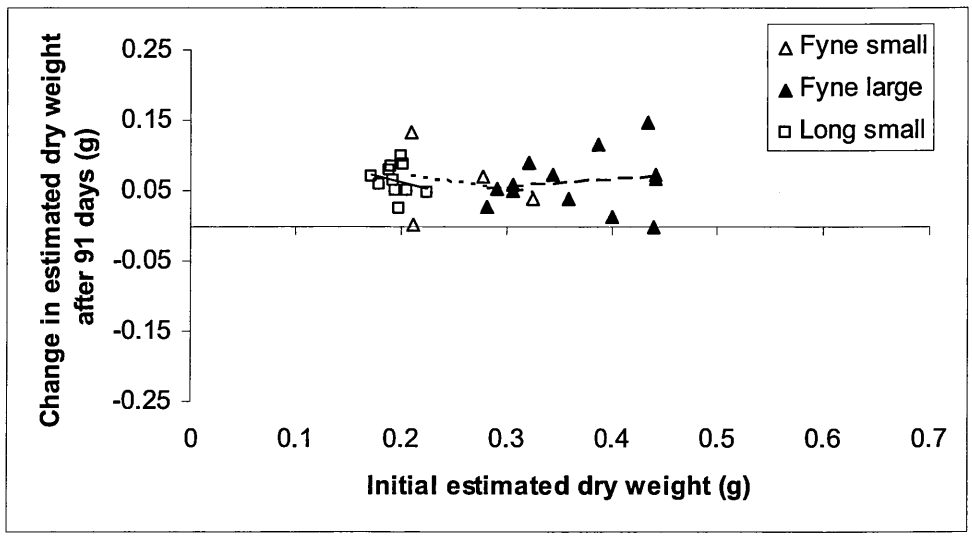


Figure 3.10 Change in estimated dry weight after 91 days for small *L. littorea* at Lochs Fyne (small dashed line, y = -0.2058x+0.114, R^2 = 0.044) and Long (solid line, y = -0.3747x+0.138, R^2 = 0.055) and large *L. littorea* at Loch Fyne (large dashed line, y = 0.1087x + 0.022, R^2 = 0.028).

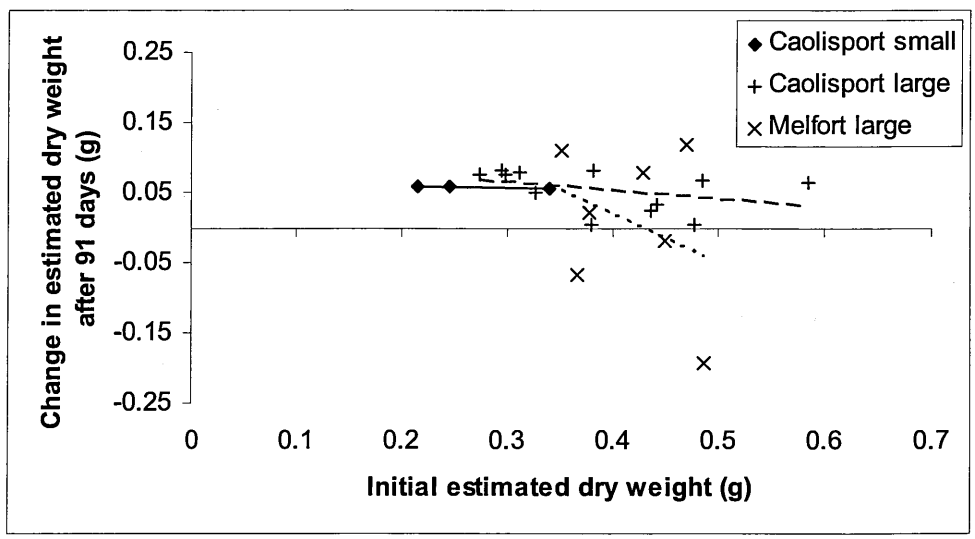


Figure 3.11 Change in estimated dry weight after 91 days for small *L. littorea* at Loch Caolisport (solid line, y = -0.0251x+0.063, R^2 = 0.996) and large *L. littorea* at Lochs Caolisport (large dashed line, y = -0.1182x+0.100, R^2 = 0.148) and Melfort (small dashed line, y = -0.6905x+0.296, R^2 = 0.112).

3.3.3 Growth rates of *P. vulgata* from long-term photographic analysis

Ford-Walford plots, derived from the von Bertalanffy growth equation (equation 9), were constructed for *P. vulgata* at each loch position looking at initial shell length against shell growth over time. Regressions were fitted to the points and an estimation of the maximum length (L_∞) was obtained using equation 10;

$$L_{(t)} = L_\infty(1-e^{-K\Delta t}) \qquad (9)$$

$$L_\infty = \frac{c}{1-m} \qquad (10)$$

where K is a growth parameter, m is the slope of the regression and c is the intercept of the regression with the y-axis. No statistical difference was found in estimated maximum lengths (χ^2 test, $\chi^2 = 1.765$, $P = 0.623$) between lochs (Figure 3.12). At the mouth of the lochs, Loch Long was found to have the fastest growth rate ($K = 0.041$ mm/month) and Loch Fyne the slowest ($K = 0.021$ mm/month). The largest maximum size predicted for *P. vulgata* was found in Loch Long ($L_\infty = 44.71$ mm at the inner and 44.18 mm at the mouth) and the smallest at the inner site of Loch Caolisport ($L_\infty = 36.11$ mm) and the mouth of Loch Melfort ($L_\infty = 34.01$ mm, Figure 3.12).

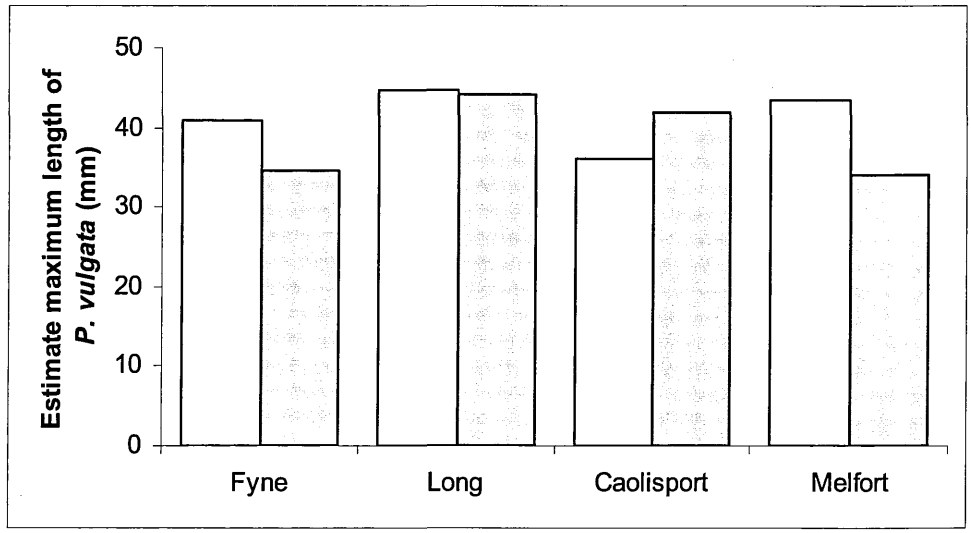


Figure 3.12 Estimated maximum shell length (L_∞) of *P. vulgata* from Ford-Walford plots at inner (open bars) and mouth (shaded bars) sites of Lochs Fyne, Long, Caolisport, and Melfort.

Measured *P. vulgata* were analysed separately according to size class with small animals having an initial shell length ≤21 mm and large animals >21 mm (Figure 3.13). A total of 26 small (mean = 16.55 mm) *P. vulgata* were measured compared with 54 large (mean = 29.07 mm) individuals. The smallest animal measured 9.87 mm and was found at the mouth of Loch Fyne with the largest animal measured at the mouth of Loch Melfort (42.08 mm). The fastest mean growth rate of small *P. vulgata* were recorded on the lower shores at the inner site of Loch Long and the slowest mean growth rate on the upper shore at the mouth of Loch Long (Figure 3.14). No significant differences were found with the covariate interactions in small *P. vulgata* (Table 3.7). Height was the only variable of the small animals found to be significant with faster growth rates recorded at MHWN from both regions.

The interaction between height and the covariate, initial length, was found to be significantly different in larger *P. vulgata* (Table 3.8). Animals at MHWN were found to have a faster mean growth rate than those at MLWN with larger animals found at the latter height (Figure 3.14). The fastest mean growth rates of large *P. vulgata* were recorded on the upper shores at the mouth of Loch Fyne with the slowest mean growth rate recorded on the upper shores at the inner site of the same loch (Figure 3.14).

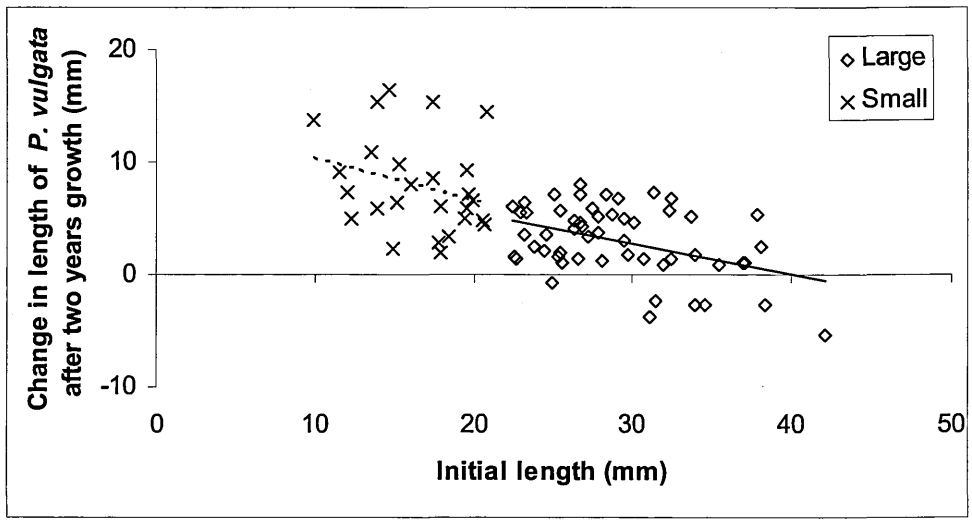


Figure 3.13 Change in length after two years of small (≤21 mm) and large (>21 mm) *P. vulgata.* Linear regressions are shown for both small (dashed line, $y = -0.38x+14.15$, $R^2 = 0.08$) and large (solid line, $y = -0.28x+11.22$, $R^2 = 0.19$) animals.

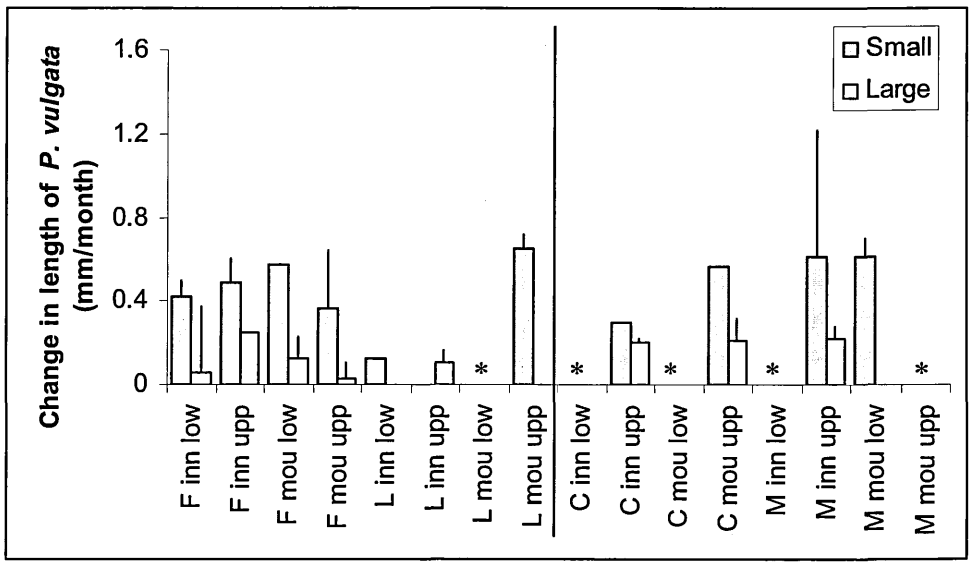


Figure 3.14 Change in length per month over two years of small (≤21 mm) and large (>21 mm) *P. vulgata.* 95% confidence intervals are shown. * = sites were not sampled.

Table 3.7 Results from a nested ANCOVA design examining differences in slopes of the initial and final length interactions of small (<21 mm) *P. vulgata.*

	d.f.	SS	MS	F ratio	P value
Region	1	5.86	47.45	0.75	0.519
Loch(Region)	2	23.67	42.29	129.29	0.981
Position	1	8.52	0.54	++	
Height	1	6.72	112.06	11.10	0.007
Initial	1	17.91	9.50	0.60	0.455
Region×Position	1	0.96	9.76	++	
Region×Initial	1	4.45	1.95	0.11	0.741
Position×Height	1	0.35	24.55	1.45	0.254
Position×Initial	1	3.65	7.69	0.45	0.514
Height×Initial	1	1.75	7.61	0.45	0.517
Position×Loch(Region)	2	4.28	5.15	0.30	0.744
Region×Position×Initial	1	1.85	1.85	0.11	0.748
Residual	11	186.38	16.94		
Total	25				

++ = denominator of the F-test was zero.

Table 3.8 Results from a nested ANCOVA design examining differences in slopes of the initial and final length interactions of large (>21 mm) *P. vulgata*.

	d.f.	SS	MS	F ratio	P value
Region	1	4.01	20.97	0.60	0.520
Loch(Region)	2	9.90	36.94	2.29	0.393
Position	1	12.56	3.31	0.24	0.689
Height	1	27.32	182.37	21.45	0.001
Initial	1	129.20	411.09	50.34	<0.001
Region×Position	1	31.94	0.27	0.02	0.896
Region×Initial	1	0.20	1.37	0.19	0.664
Position×Height	1	0.39	1.66	0.23	0.633
Position×Initial	1	11.06	0.44	0.06	0.806
Height×Initial	1	20.91	32.67	4.58	0.039
Position×Loch(Region)	2	46.53	12.45	1.74	0.189
Initial×Loch(Region)	2	8.10	1.67	0.23	0.792
Region×Position×Initial	1	30.81	30.81	4.32	0.045
Residual	37	264.13	7.14		
Total	53				

3.3.4 Growth rates of *M. edulis* from transplantation experiments

All *M. edulis* were categorized into three size classes of small (shell length <30 mm), medium (30 mm ≤ shell length ≤ 40 mm), and large (shell length >40 mm) and analysed separately. Growth rates were not found to differ within cages (nested ANCOVA, $F_{15,153} = 0.88$, $P = 0.397$).

No significant difference was found with the treatment and covariate interaction for small mussel growth rates over 203 days (ANCOVA, $F_{5,35} = 1.06$, $P = 0.397$, Appendix 3.1) although a significant difference was observed with the reduced model (ANCOVA, $F_{1,40} = 262.22$, $P<0.001$) with mussels in Loch Caolisport of an initially larger size than those in Loch Long (Figure 3.15). Small mussels transplanted from Loch Caolisport to Loch Long were found to have the slowest mean growth rate of all the treatments (Figure 3.15). Transplanting small mussels from Loch Long to Loch Caolisport increased mean growth rates compared with disturbed mussels at Loch Long. The highest growth rates of small mussels were found in the translocated treatment from Loch Caolisport. Similar significant results were found for the following 110 days (Appendix 3.2). All treatments of small mussels during this period showed positive mean growth rates with the disturbed mussels at Loch Long having the greatest mean growth rate and the mussels transplanted from Loch Long to Loch Caolisport having the slowest mean growth rates (Figure 3.16).

The interaction between treatments and the covariate of medium sized mussels was found to be significant after 203 days of growth (ANCOVA, $F_{5,78} = 2.82$, $P = 0.022$, Figure 3.15, Appendix 3.1) although no difference in the interaction was found 110 days later (ANCOVA, $F_{4,62} = 2.25$, $P = 0.074$, Figure 3.16, Appendix 3.2) with the reduced

model showing a significant difference (ANCOVA, $F_{1,66} = 706.41$, $P<0.001$). The only treatment to show a positive mean growth of medium sized mussels after 203 days was the transplant from Loch Long to Caolisport (Figure 3.15). All treatments in Loch Long showed a negative mean growth with the transplant from Loch Caolisport showing similar values to the disturbed treatment in Loch Long. Over the following 110 days, these two treatments remained similar to each other but were recorded to have a positive mean growth (Figure 3.16). The only treatment to show a negative mean growth during this time period was from disturbed mussels in Loch Caolisport which were found to be of similar value to those from over the initial 203 days (Figure 3.15 and Figure 3.16).

No significant difference was found in the interaction between treatment and the covariate of initial length in large mussels 203 days from the start of the experiment (ANCOVA, $F_{5,46} = 0.28$, $P = 0.920$, Figure 3.15, Appendix 3.1) or 110 days later (ANCOVA, $F_{4,28} = 0.68$, $P = 0.612$, Figure 3.16, Appendix 3.2). Significant differences were found in the reduced analysis for mussels 203 days (ANCOVA, $F_{1,51} = 695.91$, $P<0.001$) and 110 days later (ANCOVA, $F_{1,32} = 477.41$, $P<0.001$). Mean growth of large mussels was found to be negative for all treatments over the initial 203 days and for those treatments in Loch Caolisport over the following 110 days (Figure 3.15 and Figure 3.16). During this latter time period, the only positive mean growth was recorded at Loch Long for the disturbed and transplanted treatments, although the values were the smallest recorded (0.05 mm and 0.04 mm, respectively) throughout all treatments showing positive growth.

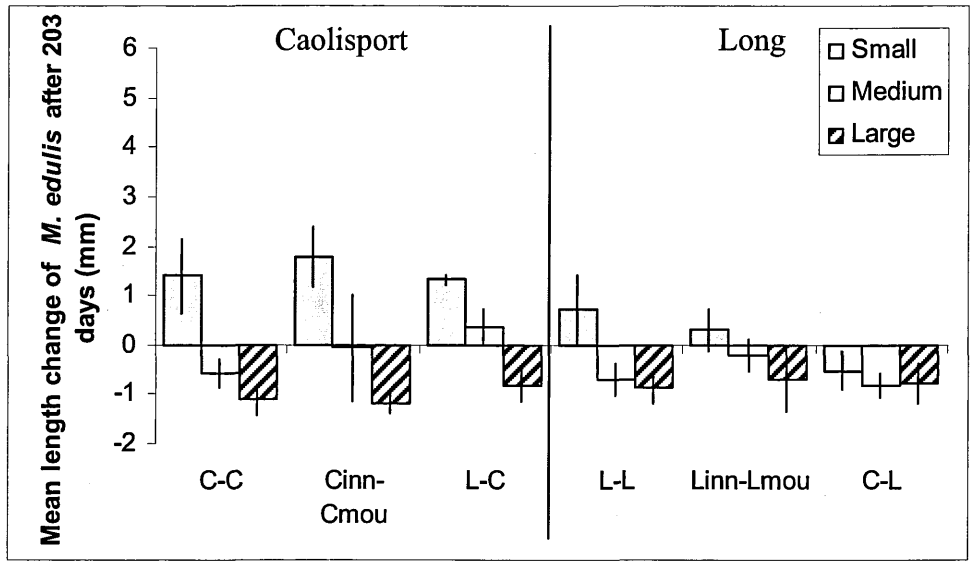


Figure 3.15 Change in shell length after 203 days of small (<30 mm), medium (≥30 mm, ≤40 mm), and large (>40 mm) *M. edulis*. Three treatments; disturbed (C-C, L-L), translocated (Cinn-Cmou, Linn-Lmou), and transplanted (L-C, C-L) are shown with 95% confidence intervals.

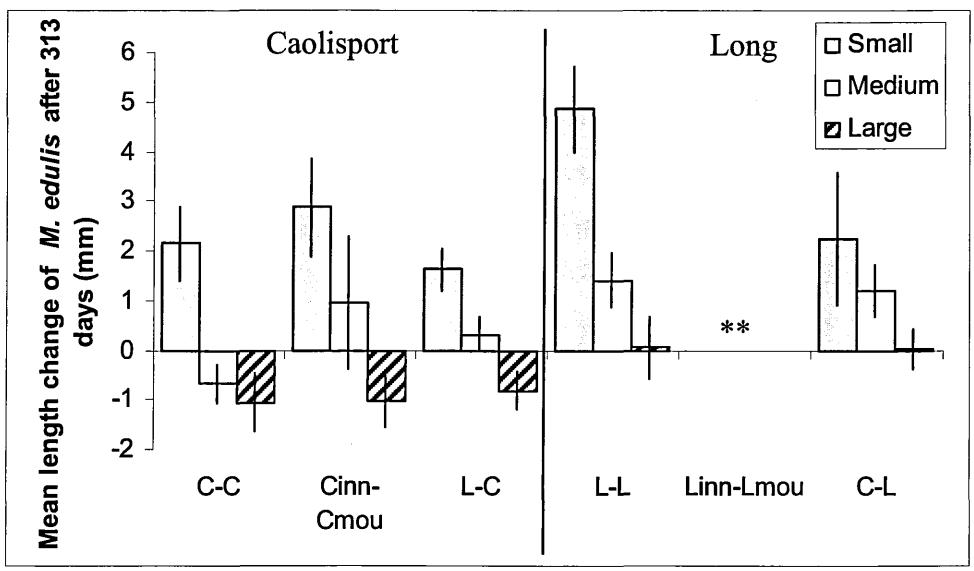


Figure 3.16 Change in shell length after 313 days of small (<30 mm), medium (≥30 mm, ≤40 mm), and large (>40 mm) *M. edulis*. Three treatments; disturbed (C-C, L-L), translocated (Cinn-Cmou, Linn-Lmou), and transplanted (L-C, C-L) are shown with 95% confidence intervals. ** = treatment lost due to removal of cages.

3.4 Discussion

Three differing types of *in situ* experiments were used in order to determine individual growth rates of three intertidal snail species, *N. lapillus*, *L. littorea*, and *P. vulgata*, and the filter feeder, *M. edulis*. With the lack of age specific data on each individual it was necessary for the experiments to be non-destructive enabling continuous measurements to be taken. Only two published studies (Palmer 1982; Burrows and Hughes 1990) have used the same technique used here to measure growth of *N. lapillus* (see sections 3.2.1 to 3.2.3). Few *in situ* studies have examined growth rates of individually marked *L. littorea* (Gardner and Thomas 1987; Yamada 1987; Petraitis 2002) and these studies only measured changes in shell dimension. Many studies have determined growth of *P. vulgata* (e.g. Jenkins *et al.* 1999b; Thompson *et al.* 2000; Jenkins and Hartnoll 2001; Boaventura *et al.* 2002a) and there was a plethora of information on the commercially farmed blue mussel, *M. edulis*, although only one published study (Honkoop *et al.* 2003) applied a similar experimental design but examined scope for growth of *Mytilus* species rather than growth rates.

3.4.1 Growth of tagged *N. lapillus* and *L. littorea*

Adult *N. lapillus* were found to have a faster growth rate on the west coast with the fastest growth rate recorded at Loch Melfort and the slowest at Loch Fyne. Both lochs are barnacle dominated (see Chapter 2). Unfortunately, only one adult was recaptured from the mussel dominated sites at Loch Long. *Nucella lapillus* feed almost exclusively on barnacles and mussels (Dayton 1971; Wieters and Navarrete 1998; Navarrete *et al.* 2000; Boaventura *et al.* 2002b) and are considered a good index of the limits of vertical

distribution of adult barnacles (Raimondi 1988). Mussels support poorer growth than barnacles (Palmer 1983; Moran *et al.* 1984) with shell growth found to be greatest on a diet of large barnacles followed by large mussels while starved whelks, and those feeding on small prey, showed little or no shell growth (Burrows and Hughes 1990). The largest mean lengths of *S. balanoides*, the dominant barnacle in this study, were recorded at Loch Melfort for the 2004 and 2005 settlements (section 2.3.4) which could explain the fast growth of *N. lapillus* observed at this loch from May to August 2004. Largest mean lengths of the established population and the 2003 settlement of *S. balanoides* were found at Loch Fyne which poses the question of whether growth rates in *N. lapillus* remain constant at each loch with the potential change in mean size of their prey over time. Faster growing snails have the potential to produce more offspring at any particular age (Etter 1996) and so, since *N. lapillus* has a closed population with no larval stage, it would be expected to find greater densities of this species on the west coast. From the preliminary investigation on species abundances (section 2.3.1) sites in the Clyde and the west coast were found to have similar abundances of *N. lapillus*. If growth rates changed over time with an initial fast growth on the west coast which was superseded one year later with a faster growth in the Clyde, corresponding with the changes in large barnacle lengths, abundances will be equal in both regions. The lack of difference in the density of *N. lapillus* between the Clyde and the west coast may be due to a reduced carrying capacity for the species within the latter region. Mortality would also be a significant contributing factor but no data were available for *N. lapillus* mortality during the study.

The general trend of this study showed that juvenile *N. lapillus* had a slightly greater change in estimated dry weight than adults although very few juveniles were caught compared with adults. Young *N. lapillus* and sub-adults, in previous studies, were

found to accumulate shell and body mass faster than adults, with growth being much greater in active-shell margined animals which in turn was found to be greater at exposed compared to sheltered sites (Burrows and Hughes 1990). Shores of intermediate exposure supported the highest growth rates of *N. lapillus* despite having the least amount of prey (Etter 1989) although this may be due to a higher assimilation efficiency or the ability to consume more of the prey tissue (Etter 1996).

Shell height (Williams 1964; Fish 1972; Petraitis 2002), growth at the shell lip (Gardner and Thomas 1987), or shell length (Kemp and Bertness 1984; Yamada 1987; Wahl 1997) were the common measurements taken in studies of *L. littorea* growth rates. These measurements do not take into account changes in flesh dry weight and, due to natural wear and tear of the shell from erosion or shell breakages, change in body mass is a better measure of somatic growth than shell size. It should be noted, however, that *L. littorea* were categorised by shell length into small and large animals, so as to minimise the effect of initial size on growth rates over time, but estimated dry weights were used in the statistical analysis. Although initial shell lengths may not have differed significantly, it is conceivable that the estimated dry weights may have been found to be significantly different due to factors such as reproductive stage, sex, or when and what the animal last ate.

Although *L. littorea* are found on shores of varying exposure, preferring more sheltered areas (Crisp and Southward 1958; Moyse and Nelson-Smith 1963) a previous study (Yamada 1987) on the east coast of North America did not find any difference in growth rates between areas of differing wave exposure. However, an increase in density (Petraitis 2002) and fouling organisms on the shell of *L. littorea* (Wahl 1997) was found to have a negative effect on growth rates. Very little fouling was observed

throughout the study area on unmarked animals (personal observation) with no fouling found on any recaptured animals. Where fouling was present at the start of the study, it was carefully removed from the shell. The fastest growth rates were found in Loch Fyne which had the second highest density recorded from photographic analysis (see section 2.3.2.6) and Loch Melfort, an area of low density from photographic analysis, was found to have the slowest growth rates. The preliminary analysis (section 2.3.1) supported these density findings with *L. littorea* found to be the 27th most abundant species at Loch Melfort compared with Loch Fyne where it was the 7th most abundant. These results suggest high densities of *L. littorea* do not have a negative effect on their growth although dense localised patches of this species were observed at Loch Melfort in crevices and under rocks which may have affected their growth rates. Further investigations would have to be carried out in order to determine whether density was a major influencing factor.

Large *L. littorea* were found to have a slower rate of growth than small animals which was supported by the literature (Williams 1964). No age data were obtained for the animals during this study with previous work suggesting few animals lived longer than three years (Gardner and Thomas 1987).

3.4.2 Growth of *P. vulgata* from digital images

This is the first known study where photographic analysis was used to measure the growth rates of *P. vulgata*. During low tide this species returns to a home scar where it remains until the tide comes in and then resumes foraging. Due to the sessile nature during low tide and that change in limpet shell length has been found to be a consistent measure of growth in *P. vulgata* across the wave exposure gradient (Jenkins and

Hartnoll 2001), analysis of successive images, as used for sessile barnacle species (section 2.2.5) was used to measure growth rates of *P. vulgata*. An added advantage of photographic analysis over fencing experiments is the lack of human intervention as fencing *Patella* species has shown to reduce their mean dry weight, probably due to the reduced foraging range imposed by the fences (Boaventura *et al.* 2002a).

Measured growth rates were categorised into small (≤21 mm) and large (>21 mm) limpets but unfortunately there were not enough data from small animals to make any comparisons with the exception that the fastest growth rates, for both size classes, were recorded in Loch Melfort and the slowest in Loch Long. Growth rates of *P. vulgata*, from a previous study, were found to range from 2 mm/year at sheltered shores to 4.4 mm/year at exposed shores (Jenkins and Hartnoll 2001) which corroborated the findings of the recorded growth rates of this study. Growth rates of large limpets were found to be similar for all four loch systems. Extremely local differences in growth have been found to exist in *Patella* species (Lewis and Bowman 1975). The abundance of *P. vulgata* throughout the study area was found to be similar at all locations (section 2.3.1) and may be why no difference in growth rates were observed between lochs. Growth rates of *P. vulgata* have been found to be higher in low density patches but no difference was found between exposed and sheltered shores (Jenkins and Hartnoll 2001). The absence of elevated growth from sheltered sites may be a result of the low level of grazing despite a higher level of food supply (Jenkins and Hartnoll 2001).

3.4.3 Transplantation of *M. edulis* to assess growth rates in the Clyde and west coast

Cages did not affect growth rates of *M. edulis* in this study or in previous studies (Dolmer 1998; Garton and Johnson 2000). Growth rates of mussels are strongly dependent on initial shell length (Garton and Johnson 2000) and so were categorised into small (<30 mm), medium (30 mm ≤ shell length ≤ 40 mm), and large (> 40 mm). The results clearly demonstrate size-dependent variation in growth rates. Small mussels were found to have the fastest growth rates for both time periods and for all treatments with the exception of those mussels transplanted from Loch Caolisport to Loch Long (Figure 3.15 and Figure 3.16). The fastest growth rates were found in disturbed treatments at Lochs Long (small mussels). The slowest positive growth rates were recorded for the transplantation from Loch Caolisport to Loch Long (large mussels). Large *M. edulis* were not found to be good indicators of growth with most of the treatments recording a negative mean growth in shell length. However, the difference in growth rates between size classes may be due to differing factors such as predation, food availability, and reproduction.

As food supply is considered to be the single most important factor in determining mussel growth rates (Seed 1976; Griffiths 1980a, 1980b; Tsuchiya 1980; Page and Ricard 1990; McQuaid and Lindsay 2000) it was surprising to find that the transplantation of small mussels to Loch Long (an area of high pelagic primary production) showed slower mean growth than the disturbed mussels at Loch Long. It was predicted that the growth rates of mussels transplanted to another loch system would match the growth rates recorded for disturbed mussels within that loch system. This was not the case for small mussels in Loch Long but was noted for small mussels in Loch Caolisport after 203 days and for medium and large mussels in Loch Long.

Studies have shown that the quality, rather than the quantity, of the food source was of more importance (Page and Ricard 1990; Penney *et al.* 2001) with laboratory experiments showing poor growth in *M. edulis* fed purely on a phytoplankton food source (Williams 1981; Page and Ricard 1990). It would be expected that young, small mussels would have a much thinner shell than older, larger mussels and so be more susceptible to predation. The slow growth rate observed in transplanted small mussels to Loch Long may be an indication that predation rates on small mussels were greater in Loch Long than in Loch Caolisport. It has been shown that when mussels are exposed to an increased predator presence, the mussels undergo predator-inducible defences such as a thickening of their shell or an increased adductor muscle (Smith and Jennings 2000; Reimer and Harms-Ringdahl 2001; Caro and Castilla 2004). Growth rates of small (20 mm shell length) and large (50 mm shell length) *M. edulis* were found to have a weak correlation with chlorophyll *a* concentration (Page and Hubbard 1987). The authors suggested that smaller mussels used non-phytoplankton food sources, such as detritus and bacteria, to support growth during periods of low phytoplankton abundance and that the lack of correlation in large mussels may be related to gonad maturation. A third possible explanation for a decrease in growth rates at a site of high chlorophyll *a* concentration was discussed by Foster-Smith (1975) and Widdows *et al.* (1979). It was suggested that a levelling off or decline in particle ingestion rates of *M. edulis* was associated with high seston concentrations and so reduced growth rates. From the results of the present study it is not possible to determine whether the slow growth rates of small mussels transplanted to Loch Long were influenced by non-phytoplankton food sources, predation, or a combination.

The fastest positive growth of medium sized mussels was recorded for the disturbed treatment in Loch Long and the slowest in the transplanted treatment to Loch Caolisport

(Figure 3.16). These findings corroborated those of Page and Hubbard (1987) who found a strong correlation between growth of medium-sized mussels (35 mm shell length) and chlorophyll *a* concentrations indicating that this length class may depend more on phytoplankton to support growth. The relationship between high phytoplankton biomass and increased growth rates of filter feeders is widely accepted (Page and Hubbard 1987; Page and Ricard 1990; Menge *et al.* 1994; Menge *et al.* 1997b; Menge *et al.* 1997a; Menge *et al.* 1999; Menge *et al.* 2002; Menge 2003). A study carried out in Canada found that the position within an embayment affected mussel growth with slower growth rates recorded at sites outside the embayment (Archambault *et al.* 1999). In the present study the embayment, loch, was substantially larger than those studied by Archambault *et al.* (1999) but similar results were found in medium sized mussels translocated from the inner site of Loch Caolisport to the mouth after 203 days (Figure 3.15). However, mussels from the same treatment showed the opposite results 110 days later with the translocated treatment found to have a greater mean growth than the mussels disturbed at the inner site (Figure 3.16). In Canada, this was explained by an increase in water velocity outside the embayments which would reduce mussel filtration rates leading to a decrease in growth rates (Sebens 1984; Leonard *et al.* 1998).

3.4.4 Summary

This study investigated growth rates of four very different intertidal species. Although *P. vulgata*, *N. lapillus*, and *L. littorea* originate from the same subclass (Prosobranchia), the latter two species were treated similarly due to their similar external morphology. As discussed previously, many studies examining growth rates of the species from this group measured changes in shell length. However, a better measure of growth is to

estimate changes in the flesh dry weight of the animal which avoids effects on shell size or mass caused by natural erosion and shell breakage. To enable measurements of each animal over time, a series of regressions were calculated linking the weight of the animal in air, weight submerged, and dry weight. This technique was not necessary for *P. vulgata* as there was no difference found between change in shell length and biomass (Jenkins and Hartnoll 2001). It was possible to measure the change in length of *P. vulgata* using photographic analysis as animals are known to return to the same home scar at each low tide period. There was no handling of animals and environmental manipulation was minimal which ensured a highly accurate measure of the natural growth rate of this species. Growth rates of the fourth species, *M. edulis*, were analysed using a transplant experiment. When examining differences in growth rates between two regions, transplantations are a preferred method for sessile species such as mussels. Transplantations were not used in the other three motile species as the movements of each species would have to be restricted with cages to ensure no cross-contamination of population characteristics.

The fastest growth rates in the Clyde were expected to be recorded in *N. lapillus* and *M. edulis* while *L. littorea* and *P. vulgata* were expected to grow faster on the west coast. Only *P. vulgata* was found to comply with this expectation.

Growth rates in mussels are highly size specific with each size class influenced by different factors. *Mytilus edulis* show an initial fast growth that decreases with size. With food regarded as the single most important factor governing growth rates of mussels (Seed 1976) it was expected that a faster growth rate would be found in Loch Long which has high pelagic primary production. Although this was the case in small mussels which were disturbed, the other size classes did not show the same pattern.

Small mussels may have been influenced by the increased predation pressures found at Loch Long while large mussels may have a reduced growth rate due to gonad maturation (Page and Hubbard 1987). It is clear that further study needs to be carried out examining growth rates of differing mussel size classes in relation to non-phytoplankton food source in combination with high phytoplankton abundance.

An increased mussel growth rate on the west coast would lead to a corresponding increased growth rate of the predator, *N. lapillus*. However, this assumes that mussels thrive on the west coast sites but, as shown in Chapter 2, mussels are scarce at these sites. Higher growth rates of this species were expected to be found at both loch sites within the Clyde and although only one *N. lapillus* was recaptured at Loch Long (the loch with the highest concentration of mussels throughout the study area), Loch Fyne was found to have the slowest growth rates. Although the results do not support the expectation of higher growth rates of *N. lapillus* in the Clyde, at a smaller temporal scale an increase in barnacle lengths were observed at Loch Melfort (section 2.3.4) which corresponded with increased growth in *Nucella*. It would therefore be conceivable that growth rates of *Nucella* would increase with an increase in bottom-up processes which would directly influence the predators' food source but over a prolonged period of time. If this were the case, increased growth rates of *Nucella* would be found to fluctuate between regions with the change in maximum barnacle shell lengths (largest mean barnacle lengths of the established and the 2003 populations were found in the Clyde and the 2004 and 2005 populations in the west coast, see Chapter 2).

Chapter 4 Regional impacts of predation by *Nucella lapillus* and grazing by *Littorina littorea*

4.1 Introduction

It has already been shown that bottom-up forces (e.g. elevated pelagic primary production, see Chapters 2 and 3) are a major influencing factor in structuring the intertidal community of the Clyde and the west coast of Scotland. Examining the growth rates (Chapter 3) of *Mytilus edulis* (L., 1758), however, suggested that predation by *Nucella lapillus* (L., 1758), a top-down factor, may also have an influencing effect on how the community is structured. This is not entirely surprising as differences in predation are strongly associated with bottom-up influences such as prey supply (Menge *et al.* 2002). Bottom-up processes have been shown to interact with top-down forces leading to a major effect on among-site variation in community structure (Leonard *et al.* 1998; Menge 2003). Predation intensity is one of the key trophic interactions in benthic-pelagic coupling, whereby the increased recruitment of filter feeders and increased productivity in areas affected by upwelling also have increased intensity of predation (Menge *et al.* 1997b; Menge *et al.* 1997a). Stable environments intensify interspecific competition due to species being able to reach their carrying capacity within those environments (Menge and Sutherland 1976). The role between the predation hypothesis and the competition hypothesis has been shown to be complementary with predation the dominant organising interaction in trophically complex communities and competition in trophically simple communities (Menge and Sutherland 1976, 1987). In simple terms these authors stated that processes structuring an initial intertidal community of three trophic levels, with *Nucella* species at the highest trophic level, were dominated by competition. When a fourth trophic level, predators of *Nucella* species was introduced, the community altered to a predator dominated one. Differences between west and east coasts of the United States showed

that the east coast was trophically simpler, competition dominant, and the west coast was trophically complex, predator dominant, (Menge and Sutherland 1976, 1987).

As mentioned previously (Chapter 3), *Nucella* species feed almost exclusively on barnacles and mussels (Dayton 1971; Wieters and Navarrete 1998; Navarrete *et al.* 2000; Boaventura *et al.* 2002b) with mussels supporting less growth than large barnacles (Palmer 1983; Moran *et al.* 1984; Burrows and Hughes 1990). A strong correlation exists between the abundance of sessile invertebrates, such as mussels, and whelk density (Underwood and Fairweather 1986; Menge *et al.* 1999; Navarrete *et al.* 2000). Wave exposure has been shown to be a significant factor involved in the rate of prey consumption, with whelks at exposed sites found to be more voracious (Menge 1978; Burrows and Hughes 1990; Menge 2003). Although many predators are known to feed on mussels and barnacles in the intertidal (see, Kitching *et al.* 1959; Dayton 1971; Menge 1976; Kendall *et al.* 1985; Rangeley and Thomas 1988; Guillemette *et al.* 1992; Burrows *et al.* 1999b; Beadman *et al.* 2002), it is thought that they probably have a minimal effect on predation intensity in the mid intertidal with the exception of *Nucella* (Menge 1978).

Many studies have examined the feeding strategy of dogwhelks on barnacles and mussels (Palmer 1982; Hughes and Dunkin 1984; Petraitis 1987; Burrows and Hughes 1990; Palmer 1990; Burrows and Hughes 1991; Rovero *et al.* 1999) with the predator penetrating the shell of the prey either via a drill hole (Ebling *et al.* 1964; Palmer 1983; Hunt and Scheibling 1998b) or by inserting the proboscis between mussel valves (Ebling *et al.* 1964). Dogwhelks which prey mainly on barnacles have been shown to prise open the opercular valves rather than drilling a hole (Connell 1961a) presumably since the latter action is more time consuming. Problems arise when the prey species

changes from barnacles to mussels, which are accessed with greater ease via drilling, and the dogwhelk has to either learn how to drill through the mussel's shell or prise open the valves (as described by Ebling *et al.* 1964; and Hughes and Dunkin 1984). When the situation was reversed, the main prey item changing from mussels to barnacles, dogwhelks were found to continually drill barnacle shells rather than choosing the faster entry method of prising open the opercular valves (Connell 1961a).

The major intertidal grazers found throughout the study area (see Chapter 2) were *Littorina littorea* (L., 1758) and *Patella vulgata* (L., 1758). Both these species have been shown to play significant roles in structuring intertidal communities with *P. vulgata* regulating the recruitment of macroalgae through consumption of early macroalgal stages (Anderson and Underwood 1997; Jenkins and Hartnoll 2001) and so increasing the settlement rate of *Semibalanus balanoides* (L., 1767) (Hawkins and Hartnoll 1983). *Littorina littorea* are able to affect species diversity and algal abundance (Lubchenco 1978; Southward 1978; Anderson and Underwood 1997; O'Connor and Crowe 2005). A decline in algal canopy cover causes direct and indirect effects on sessile invertebrates such as barnacles (Bertness 1984; Anderson and Underwood 1997) by reducing shelter from desiccation and increasing competition for space resulting in increased growth rates and recruitment. It is well known that herbivorous snails have a direct effect on barnacle mortality through bulldozing (Connell 1961a; Dayton 1971; Hawkins 1983; Bertness 1984). Although *L. littorea* is classed as a herbivore feeding mainly on early successional or ephemeral algae (Lubchenco 1978; Bertness 1984; Buschbaum 2000), it is a generalist grazer which uses its radula like a broom to sweep superficial diatoms and small algal fronds from the substrate (Bertness 1984) as well as inadvertently dislodging and consuming settled barnacle larvae (Buschbaum 2000).

The main aim of this chapter was to determine what effects the predator, *N. lapillus*, and the grazer, *L. littorea*, had on the community structure of a filter feeder dominated area, the Clyde, and a macroalgal dominated area, the west coast. Caged enclosures were used with half the enclosed area cleared of all flora and fauna prior to the main barnacle settlement peak (see Chapter 2). Initially *N. lapillus*, *L. littorea*, or a combination of the two species were placed within cages over three months in order to determine the influence which the predator and grazer had on barnacle recruitment and algal abundance. As *N. lapillus* prey on both barnacles and mussels, a second experiment was run in order to test the rate of predation on different sized mussels within each region. It was hypothesised that barnacle recruitment would be directly influenced by both the predator and the grazer with mortality directly influenced by predators and a potential indirect influence from grazers. An increase in algal cover would be expected with an absence of grazers and predators having no effect on algae. Relating these interactions with the already examined bottom-up forces and competition (see Chapters 2 and 3) will enable a more thorough understanding of the differences in community structure of the west coast and the Clyde and whether the regions are dominated by predation, competition, or a combination. Three null hypotheses were constructed:

- Barnacle recruitment intensity will not alter in the presence/absence of a predator, *Nucella lapillus*.
- *Littorina littorea* will have no effect on algal abundance, with no difference found between the west coast and the Clyde.
- No difference will be found in rates of predation on barnacles or the mussel, *Mytilus edulis*, between the west coast and the Clyde.

4.2 Materials and Methods

Sites midway along (termed inner) four lochs (Long and Fyne in the Clyde system, and Melfort and Caolisport on the west coast; see Chapter 2 for descriptions) were selected for determination of the effects of predation by *Nucella lapillus* and grazing by *Littorina littorea* on the intertidal community. Sites at the inner position of lochs were chosen for ease of access so as to increase time spent at each site while decreasing the distance between sites and the laboratory.

A total of five treatments were chosen, each replicated three times per site and located at mid tide level (MTL):

1. Caged, no predators, no grazers (-P -G)
2. Caged, no predators, grazers (-P +G)
3. Caged, predators, no grazers (+P -G)
4. Caged, predators, grazers (+P +G)
5. Un-caged but marked area (?P ?G)

By experimentally manipulating both *N. lapillus* and *L. littorea* it was possible to examine the effects of predation (treatment 3), grazing (treatment 2), and any potential interaction (treatment 4) which may occur between the two species. Controls (treatments 1 and 5) accounted for any cage effects. Each cage measured 60 mm x 120 mm x 30 mm with a 30 mm lip round the edge and a 10 mm mesh size constructed of stainless steel. Half of the caged area was scraped clean while the other half was left un-scraped (see Figure 4.1). Each treatment contained one animal except treatment 4 which contained one *Nucella* and one *Littorina*. Each cage was secured to the rock with four 8 mm brass screws, rawl plugs and plastic washers (Figure 4.2). Holes were drilled with a 24V cordless hammer drill. The experiment was run from March 2005 to June

2005. Treatments were photographed before and after scraping and thereafter each month with fresh animals placed back in the relevant cage after each photograph. A Ricoh Caplio RR30 digital camera (2048 normal picture quality) was used to take all photographs. Each image was rotated to the same orientation as the first image to facilitate comparisons (see section 2.2.3). A grid was overlaid onto each picture and species abundances were estimated as carried out in section 2.2.4 for the 30x30 cm abundance estimates.

Statistical analysis was carried out with a combination of summary statistics and monthly nested ANOVA, as described in Chapter 2.

4.2.1 Estimation of the rates of predation on *Mytilus edulis* by *Nucella lapillus*

Predation rates of *N. lapillus* on *M. edulis* were measured between June and July 2005 using the same cages as above (Figure 4.2). All fauna and flora were scraped off the substrate within the caged area using a paint scraper and wire brush. One *Nucella* was placed within each cage. Mussels were divided into three size classes, namely, small, medium, and large, with average total shell lengths of 35 mm (range 17 to 24 mm), 46 mm (range 22 to 34 mm), and 53 mm (range 44 to 62 mm), respectively. A cage contained either four large mussels or five of either medium or small mussels with each size class replicated four times at each site, except Loch Fyne where there were only three replications per size class due to the unusually hard substrate at this site which limited the number of holes which could be drilled. At the end of the study period empty mussel shells were examined for drill holes and all live mussels were counted.

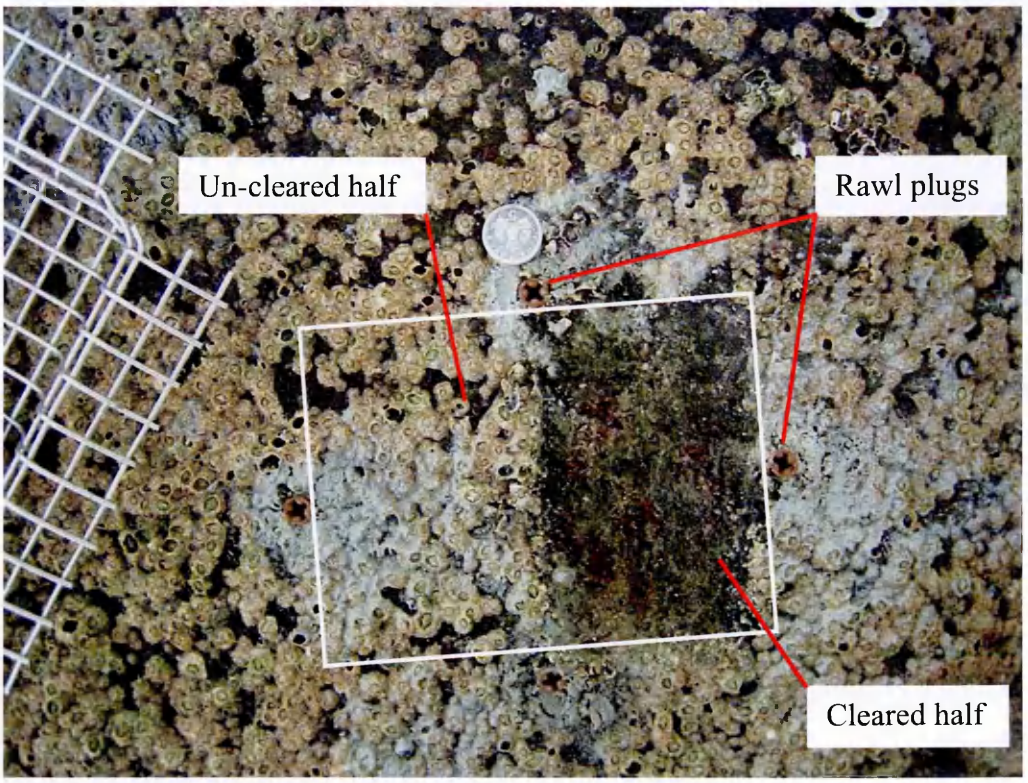


Figure 4.1 A picture of a caged area, prior to the start of the experiment, in Loch Long after clearing half of the area. The white box represents the area enclosed by the cage (see Figure 4.2 below). The coin measures 18.0 mm in diameter.

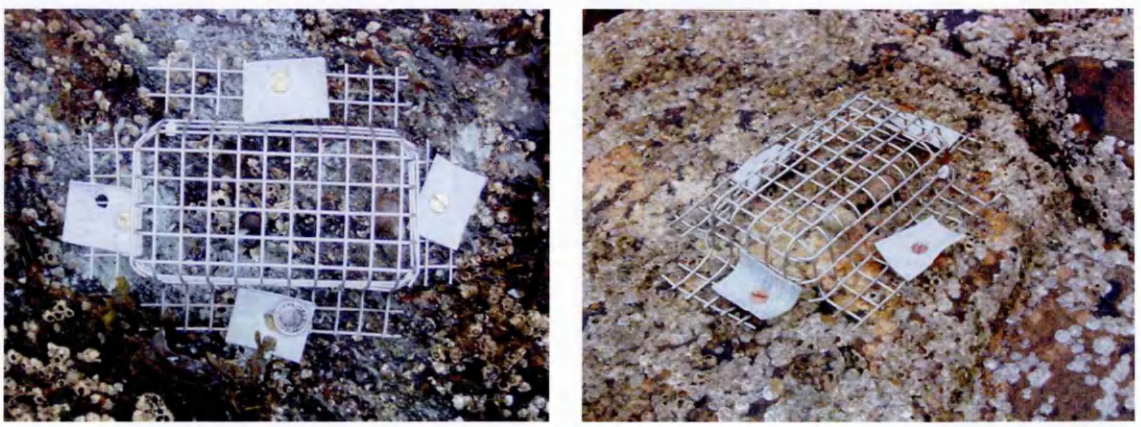


Figure 4.2 A top (left) and side view (right) of the stainless steel cages used to exclude and include predators and grazers.

4.3 Results

4.3.1 Predation and grazing pressures on barnacle populations within caged enclosures

Monthly analysis confirmed the findings of the summary statistics with more barnacle cover found in cages containing a grazer, *L. littorea* (+G), than those with a predator, *N. lapillus* (+P), (nested ANOVA; summary statistics, $F_{1,9} = 10.69$, $P = 0.010$, Appendix 4.1; 1st month, $F_{1,67} = 4.22$, $P = 0.044$, Appendix 4.2; 2nd month, $F_{1,67} = 9.01$, $P = 0.004$, Appendix 4.3; 3rd month, $F_{1,67} = 13.04$, $P = 0.001$, Appendix 4.3; see Figure 4.3 to Figure 4.6). Cages with the highest average barnacle cover were those which excluded both predators and grazers while those which only contained *N. lapillus* were found to have the lowest average barnacle cover.

Recruitment of *S. balanoides* was found to occur from mid to late April (corresponding with the 1st month of the present study) in the Clyde and early April on the west coast (see section 2.3.3). Average barnacle cover in cleared halves of all cage treatments were found to have a similar trend to that at the start of the experiment in Lochs Long and Caolisport (Figure 4.4b and Figure 4.5b, respectively). A distinct trend was noted in barnacle cover from the initial sampling and three months later in Lochs Fyne and Melfort (Figure 4.3b and Figure 4.6b, respectively). An exception in Loch Fyne was noted in the caged treatment where both predators and grazers were excluded (-P-G).

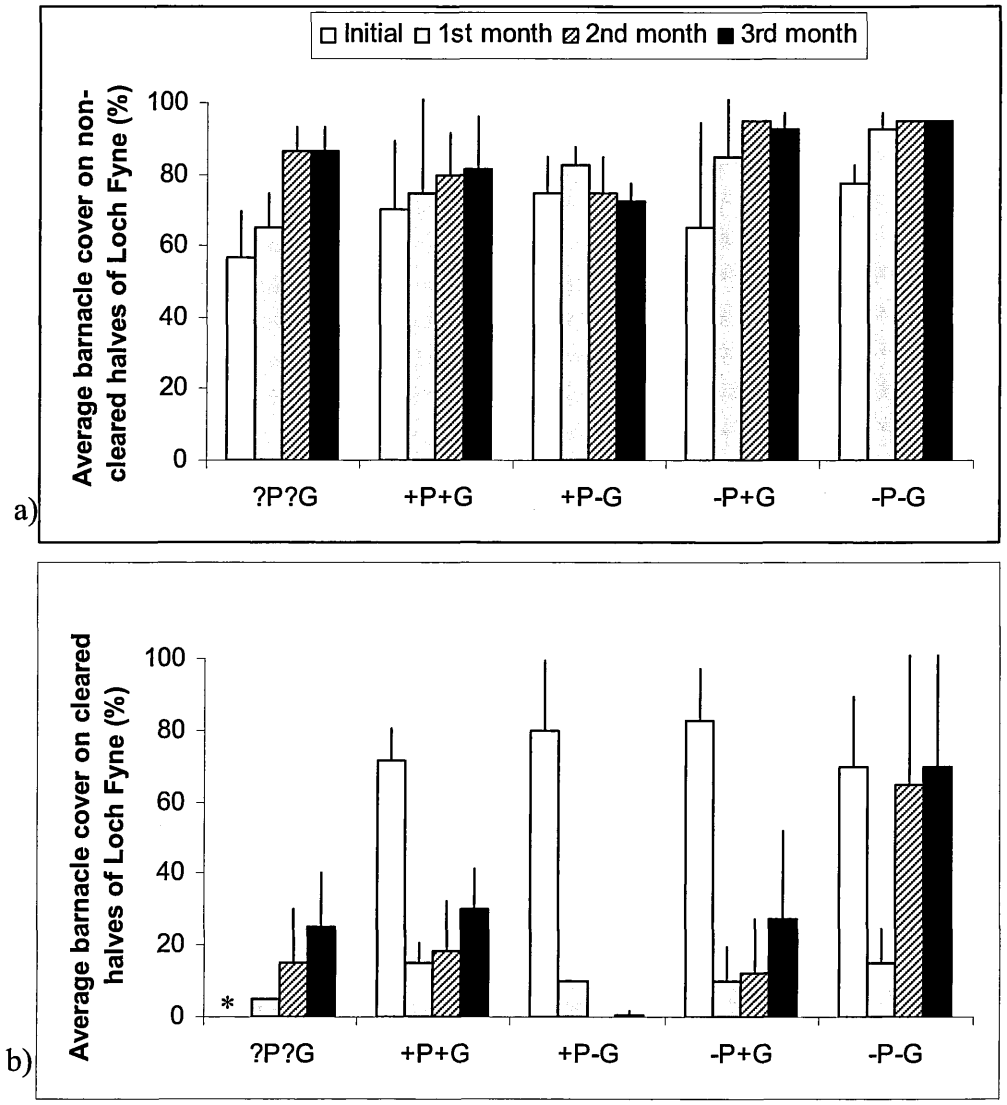


Figure 4.3 Average barnacle cover of non-cleared (a) and cleared (b) halves of the four cage treatments in Loch Fyne. Predators present (+P), predators absent (-P), grazers present (+G), grazers absent (-G), and unknown predators and grazers (?P?G) are shown for each month sampled with 95% confidence intervals. Initial sampling of average cover in cleared halves corresponds with cover prior to clearing. * denotes missing data.

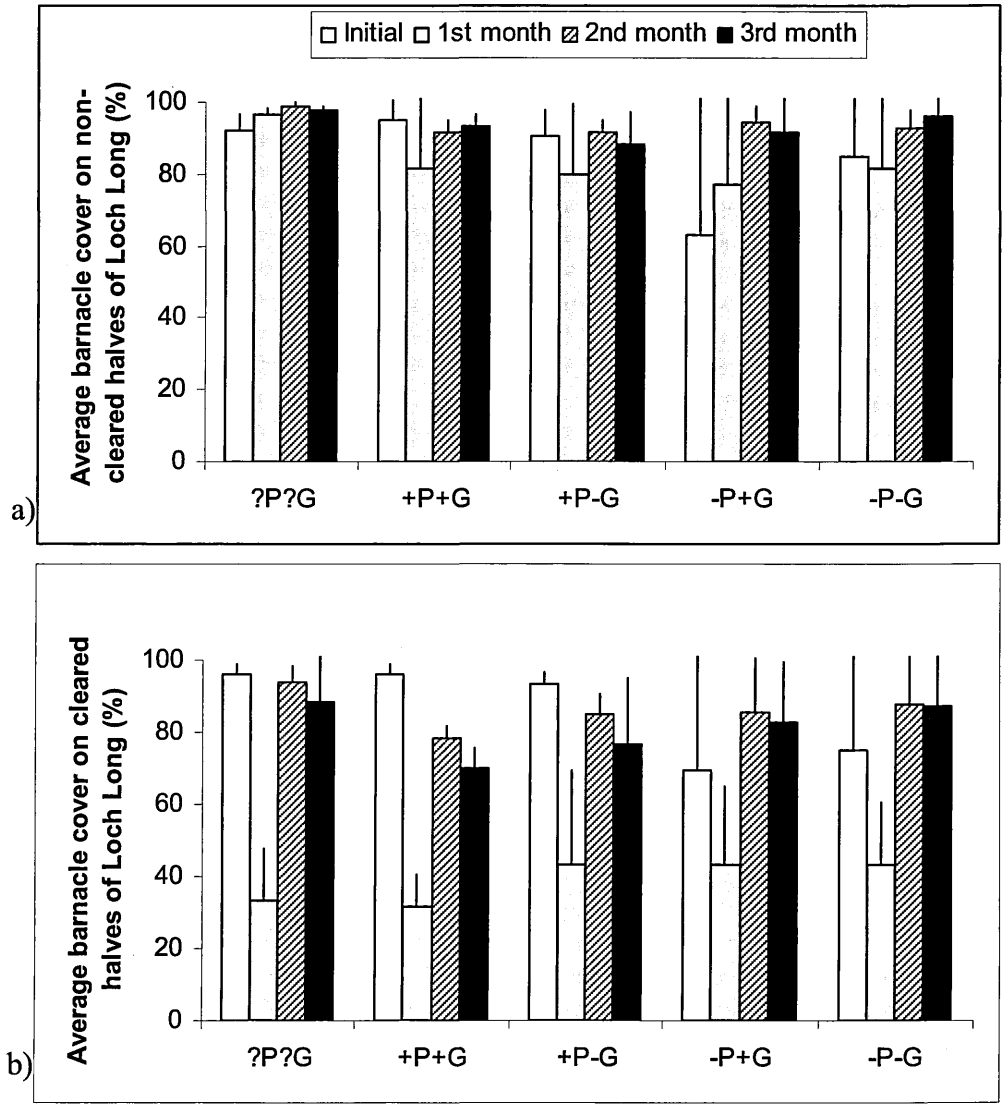


Figure 4.4 Average barnacle cover of non-cleared (a) and cleared (b) halves of the four cage treatments in Loch Long. Predators present (+P), predators absent (-P), grazers present (+G), grazers absent (-G), and unknown predators and grazers (?P?G) are shown for each month sampled with 95% confidence intervals. Initial sampling of average cover in cleared halves corresponds with cover prior to clearing.

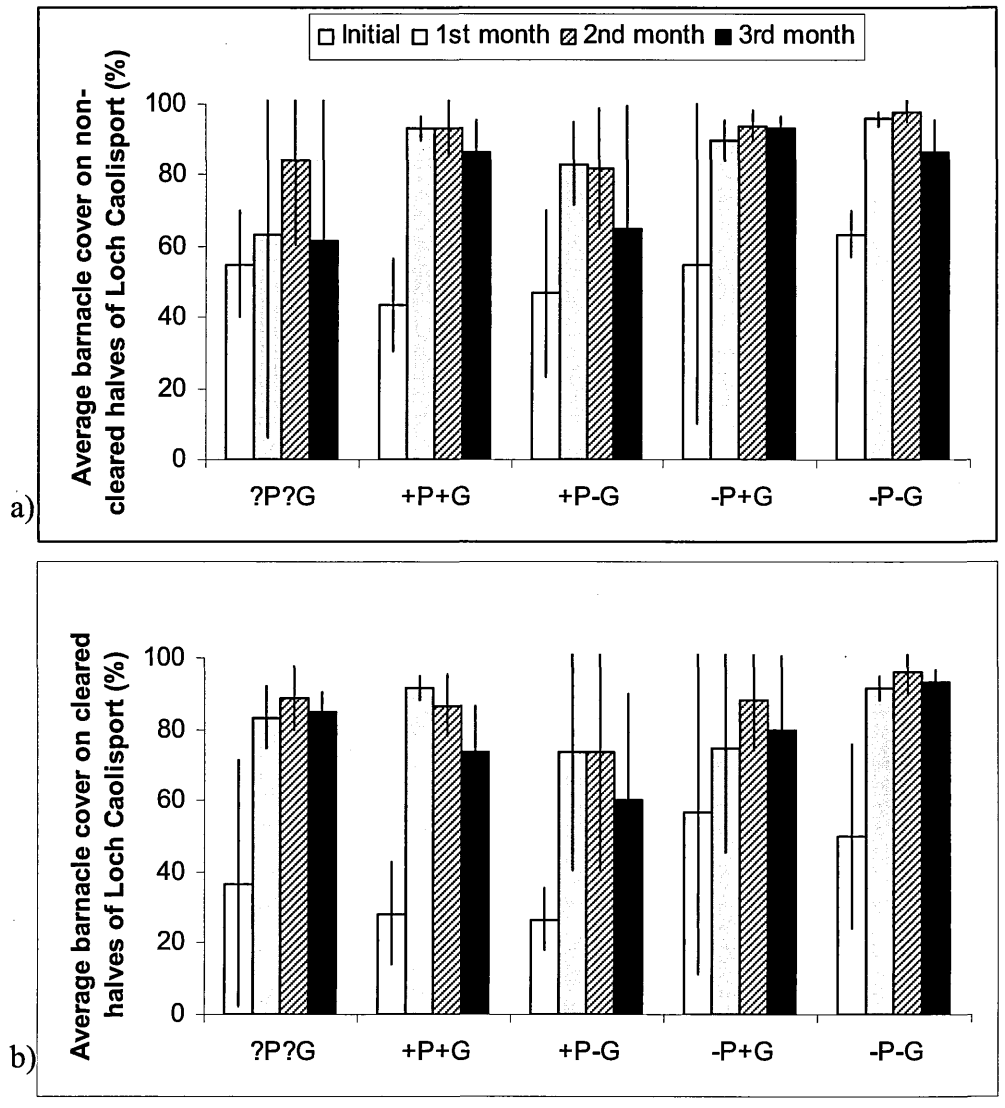


Figure 4.5 Average barnacle cover of non-cleared (a) and cleared (b) halves of the four cage treatments in Loch Caolisport. Predators present (+P), predators absent (-P), grazers present (+G), grazers absent (-G), and unknown predators and grazers (?P?G) are shown for each month sampled with 95% confidence intervals. Initial sampling of average cover in cleared halves corresponds with cover prior to clearing.

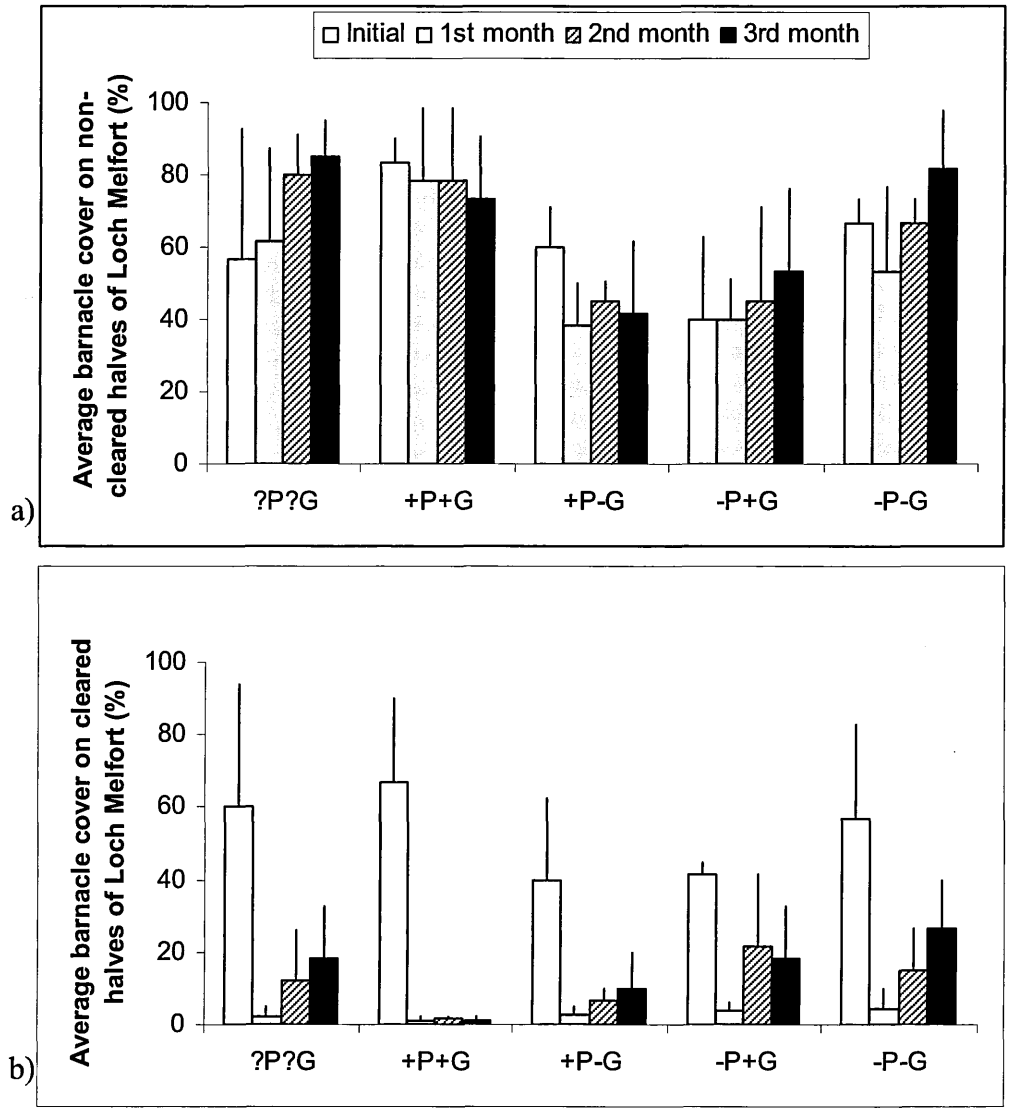


Figure 4.6 Average barnacle cover of non-cleared (a) and cleared (b) halves of the four cage treatments in Loch Melfort. Predators present (+P), predators absent (-P), grazers present (+G), grazers absent (-G), and unknown predators and grazers (?P?G) are shown for each month sampled with 95% confidence intervals. Initial sampling of average cover in cleared halves corresponds with cover prior to clearing.

The number of empty barnacle tests were counted within each cage to give a more direct measure of predation by *N. lapillus*. The majority of empty tests were recorded in the non-cleared half of the cage with empty tests becoming evident on the cleared half of the cage three months from the start of the experiment. A general trend of more empty barnacle tests were found in the Clyde system. Loch Long had the highest average number of empty barnacle tests (mean = 8.7, maximum 52, Figure 4.7b) with slightly lower values recorded in Lochs Fyne (mean = 5.2, maximum 38, Figure 4.7a), Caolisport (mean = 5.1, maximum 31, Figure 4.8a), and Melfort (mean = 3.5, maximum 22, Figure 4.8b). The presence of *N. lapillus* significantly increased the number of empty barnacle tests (nested ANOVA, summary statistics, $F_{1,9} = 28.35$, $P = 0.034$). These results were corroborated two months from the start of the experiment (nested ANOVA, $F_{1,67} = 29.34$, $P = 0.031$, Appendix 4.6) as well as the following month, although not at $P<0.05$ (nested ANOVA, $F_{1,67} = 17.19$, $P = 0.053$, Appendix 4.6). No effect was found at the initial (nested ANOVA, $F_{1,67} = 6.52$, $P = 0.104$, Appendix 4.5) or first month (nested ANOVA, $F_{1,67} = 11.14$, $P = 0.079$, Appendix 4.5) sampling.

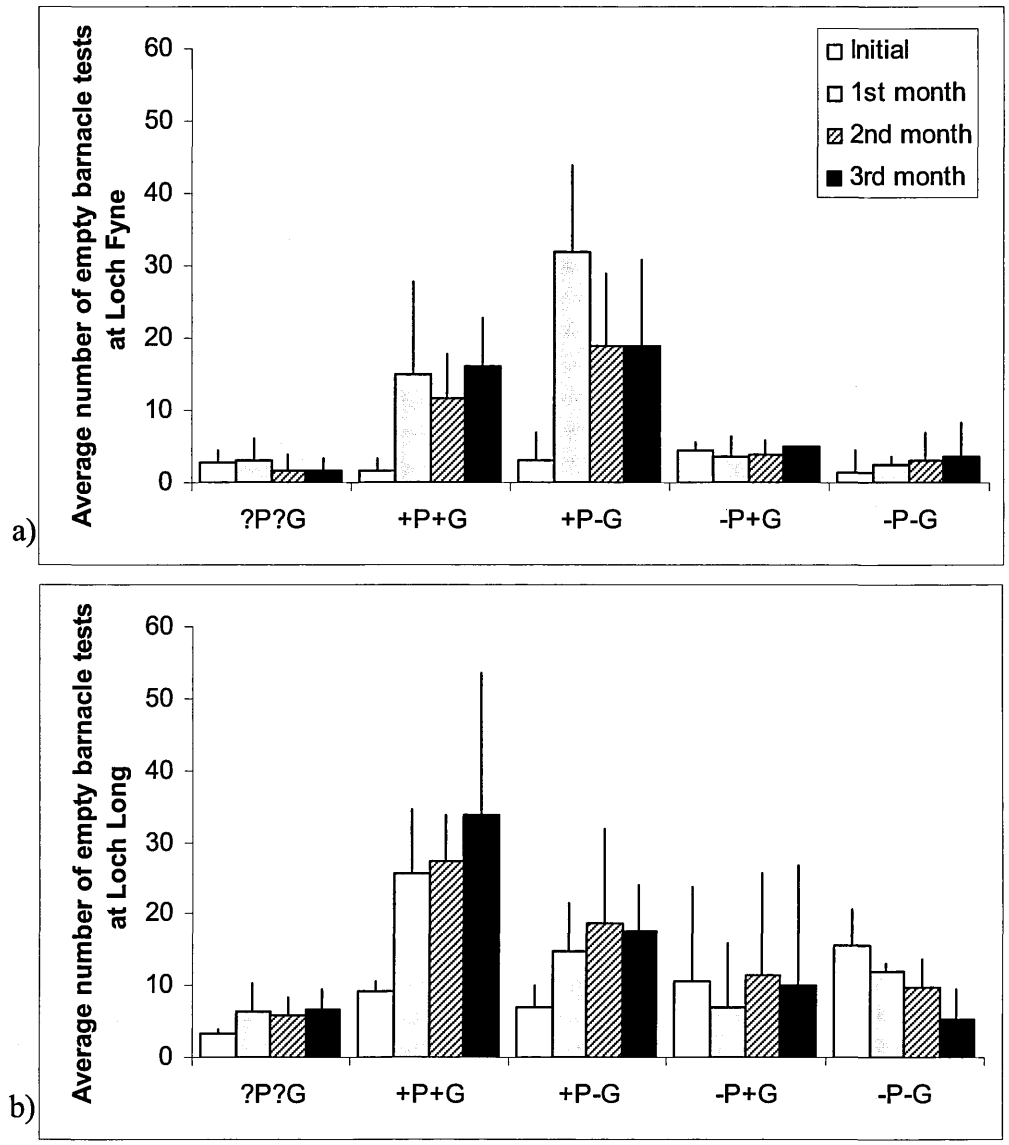


Figure 4.7 Average number of empty barnacle tests in non-cleared halves of the four cage treatments in Lochs Fyne (a) and Long (b). Predators present (+P), predators absent (-P), grazers present (+G), grazers absent (-G), and unknown predators and grazers (?P?G) are shown for each month sampled with 95% confidence intervals.

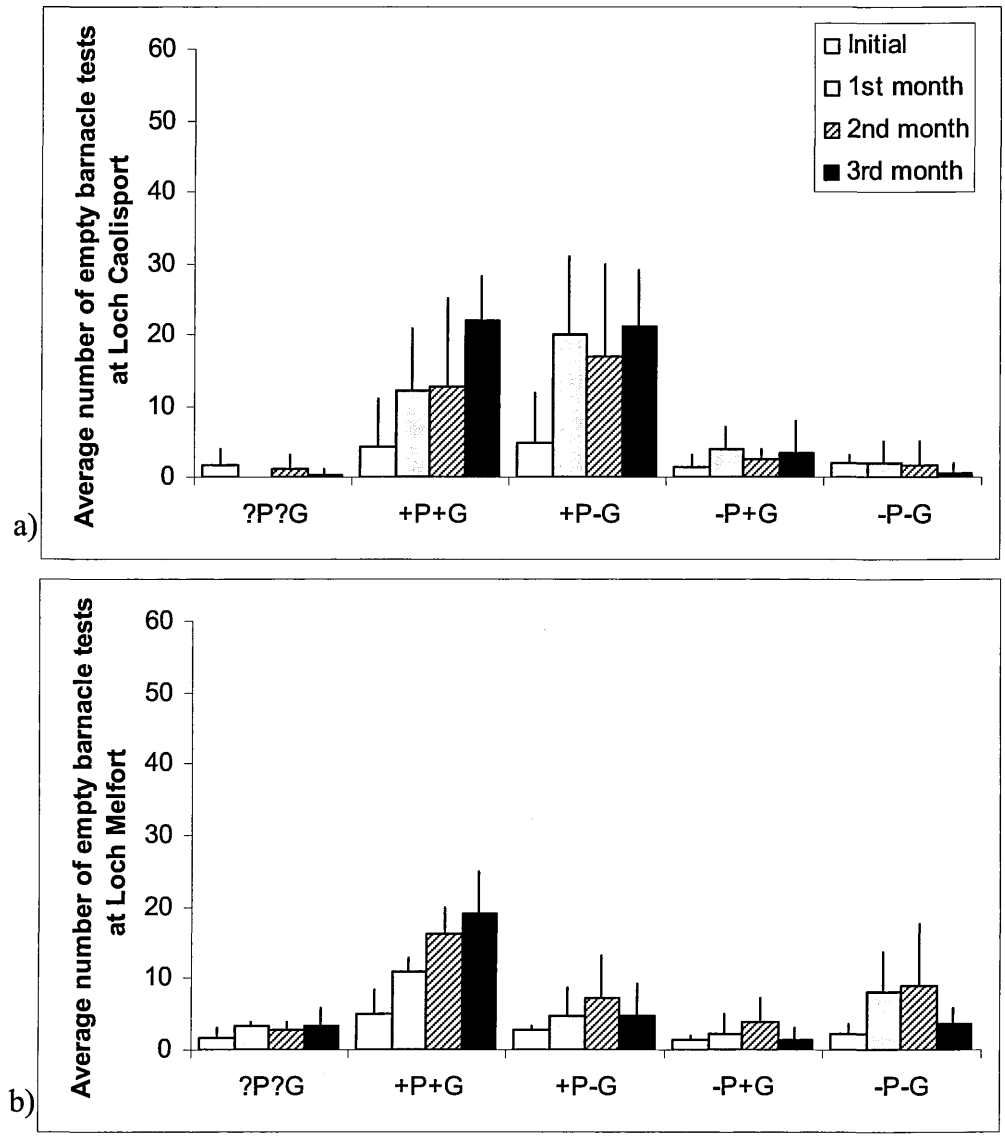


Figure 4.8 Average number of empty barnacle tests in non-cleared halves of the four cage treatments in Lochs Caolisport (a) and Melfort (b). Predators present (+P), predators absent (-P), grazers present (+G), grazers absent (-G), and unknown predators and grazers (?P?G) are shown for each month sampled with 95% confidence intervals.

4.3.2 Predation and grazing pressures on macroalgal and biofilm cover

Germlings of *Fucus vesiculosus* were recorded one month from the start of the experiment in all cage treatments at Loch Caolisport and were not noted prior to the beginning of the experiment (Table 4.1). No germlings were recorded within cages at any of the other lochs under study. No significant differences in the number of germlings recorded were found in relation to treatment type or cleared areas within Loch Caolisport (Table 4.2). Similar results were found for macroalgal cover (see Table 4.3 for the results of the three-way ANOVA) which were only found within cages at Loch Caolisport.

Table 4.1 *Fucus vesiculosus* germling total number (mean ±SD) at Loch Caolisport within the four treatment cages of predators present (+P), predators absent (-P), grazers present (+G), and grazers absent (-G). Numbers of cages per treatment are also shown (n).

	1st month		2nd month		3rd month	
Treatment	**Total (mean ±SD)**	**n**	**Total (mean ±SD)**	**n**	**Total (mean ±SD)**	**n**
+P+G	6 (3 ±2.8)	2	4 (2 ±1.4)	2	1	1
+P-G	11 (5.5 ±6.4)	2	3 (1.5 ±0.7)	2	2	1
-P+G	7 (2.3 ±1.2)	3	0	0	4	1
-P-G	6 (3 ±2.8)	2	4	1	6 (2 ±1)	3
Total	30	9	11	5	13	6
Mean	7.5		2.8		3.3	

Table 4.2 Three-way ANOVA results of germling number within cages at Loch Caolisport.

	d.f.	SS	MS	F ratio	P value
Cleared	1	3.668	3.668	0.61	0.452
Predator	1	1.321	1.321	0.22	0.649
Grazer	1	1.321	1.321	0.22	0.649
Cleared×Predator	1	1.973	1.973	0.33	0.579
Cleared×Grazer	1	0.408	0.408	0.07	0.800
Predator×Grazer	1	0.147	0.147	0.02	0.879
Cleared×Predator×Grazer	1	8.625	8.625	1.42	0.256
Residual	12	72.750	6.062		
Total	19				

Table 4.3 Three-way ANOVA results of macroalgal cover within cages at Loch Caolisport.

	d.f.	SS	MS	F ratio	P value
Cleared	1	175.0	175.0	0.62	0.453
Predator	1	300.0	300.0	1.07	0.332
Grazer	1	24.1	24.1	0.09	0.777
Cleared×Predator	1	2.1	2.1	0.01	0.934
Cleared×Grazer	1	227.3	227.3	0.81	0.395
Predator×Grazer	1	243.0	243.0	0.86	0.380
Residual	8	2250.0	281.3		
Total	14				

A disscolouration in barnacle tests was found within cages of all four loch systems and although not identified, was regarded as biofilm (Figure 4.9). Average biofilm cover was estimated, by eye, as a percentage in relation to the amount of cover recorded on barnacles. A greater cover was noted in the Clyde system (mean = 22.1%, maximum of 100%, Figure 4.10 and Figure 4.11) which was found to differ significantly from the west coast (mean = 0.4%, maximum of 10%) one month after the start of the experiment (nested ANOVA, $F_{1,67} = 27.27$, $P = 0.034$, Appendix 4.7). The presence of *N. lapillus* (+P) throughout the study area was found to significantly increase the biofilm cover (nested ANOVA; summary statistics, $F_{1,9} = 114.68$, $P = 0.009$, Appendix 4.7; 2nd month, $F_{1,67} = 139.42$, $P<0.001$, Appendix 4.8). The absence of *L. littorea* in Lochs Fyne and Caolisport but presence in Loch Long (nested ANOVA; summary statistics, $F_{2,9} = 6.38$, $P = 0.019$; 3rd month, $F_{2,67} = 3.52$, $P = 0.035$, Appendix 4.8) were also found to significantly increase the biofilm cover. A greater density of biofilm cover was found on barnacles in areas which were not cleared (nested ANOVA; summary statistics, $F_{2,9} = 7.94$, $P = 0.010$; 2nd month, $F_{2,67} = 7.99$, $P = 0.001$; 3rd month, $F_{2,67} = 3.30$, $P = 0.043$). The non-cleared halves of the cages consisted of a greater proportion of older barnacles.

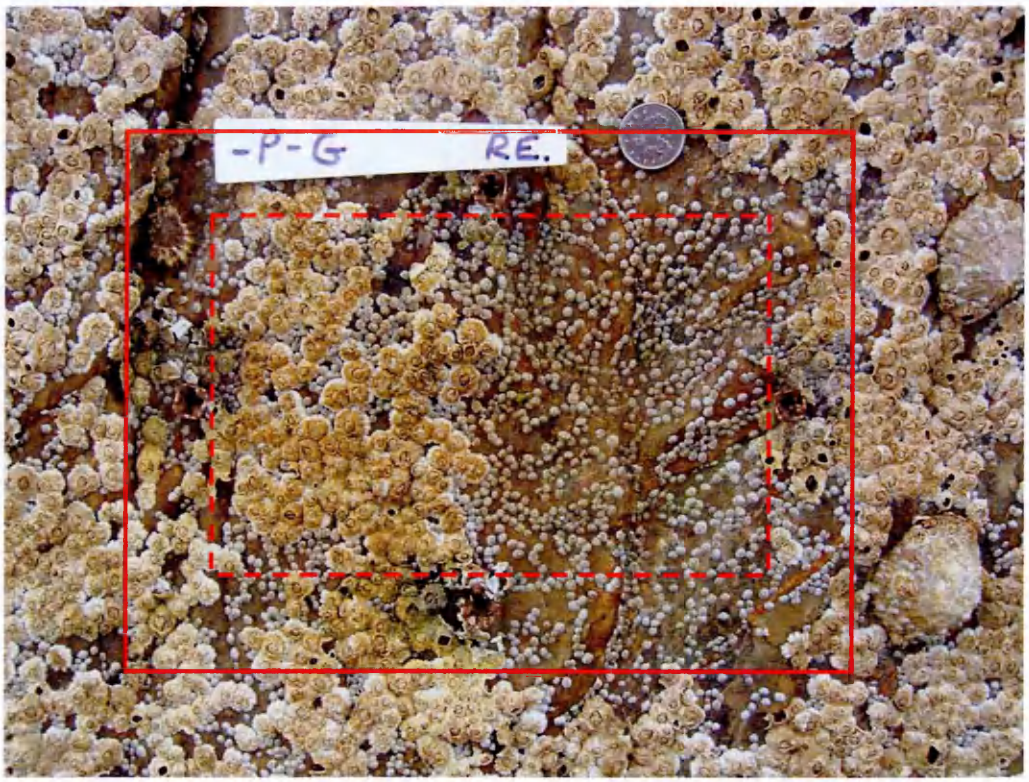


Figure 4.9 A caged area from Loch Fyne which contained no predators or grazers showing the discolouration of the barnacles within the cage. The area between the solid outer red box and the dashed inner box represents the lip of the cage with the inner dashed box, the experimental area.

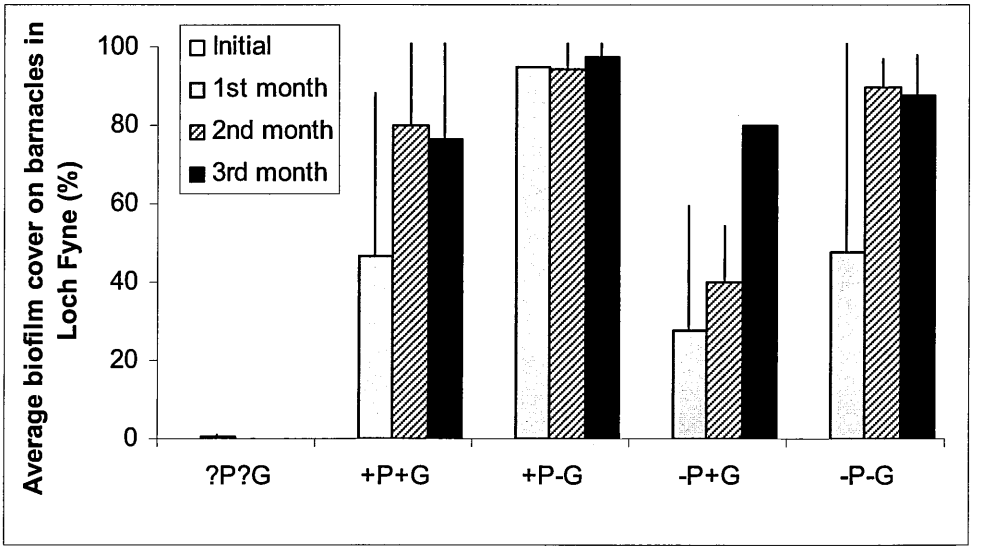


Figure 4.10 Average cover of biofilm on non-cleared halves of cages at Loch Fyne. The four treatment cages of predators present (+P), predators absent (-P), grazers present (+G), and grazers absent (-G) are shown along with the un-caged treatment (?P?G). Four sampling periods are represented with 95% confidence intervals.

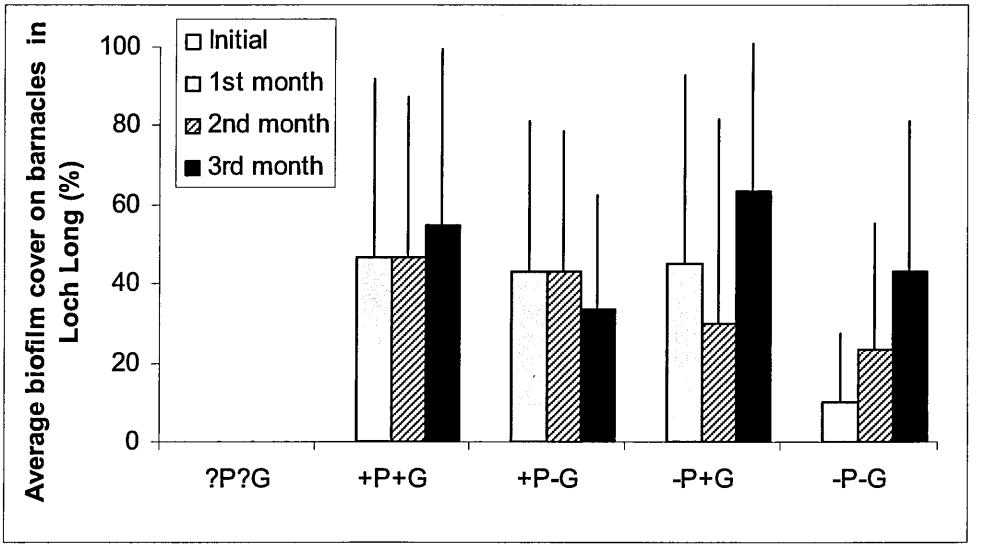


Figure 4.11 Average cover of biofilm on non-cleared halves of cages at Loch Long. The four treatment cages of predators present (+P), predators absent (-P), grazers present (+G), and grazers absent (-G) are shown along with the un-caged treatment (?P?G). Four sampling periods are represented with 95% confidence intervals.

4.3.3 Rates of predation on *Mytilus edulis* by *Nucella lapillus*

Over the one month study period examining the rates of predation on *M. edulis* by *N. lapillus*, 14.4% of the total number of mussels in all four lochs were found to have been preyed on. Only three mussels (shell lengths of 24.4 mm, 27.9 mm, and 29.3 mm), from Loch Fyne, were found to have a drill hole in their shell with the remainder showing signs of shell breakage along the shell seal of the mussel. Significantly more mussels were found to have been preyed on at lochs in the west coast compared to those of the Clyde ($\chi^2 = 5.154$, $P = 0.023$) with no significant difference found in predator size (shell length of *N. lapillus*) between regions (nested ANOVA, $F_{1,31} = 0.09$, $P = 0.795$) or mussel size classes (nested ANOVA, $F_{2,31} = 1.63$, $P = 0.304$, Figure 4.12).

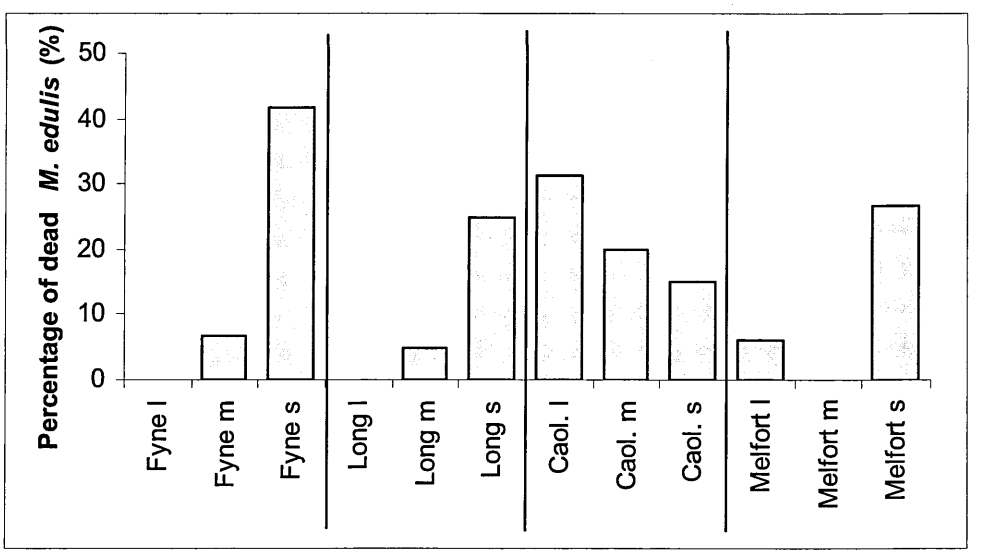


Figure 4.12 Predation rates of *N. lapillus* on three size classes, large (l), medium (m), and small (s) of *M. edulis* at Lochs Fyne, Long, Caolisport, and Melfort.

4.4 Discussion

No regional variation was recorded in barnacle cover under any of the treatment conditions although there was a general trend in empty barnacle tests with the greatest mean numbers recorded at Loch Long (mean = 8.7) and the lowest mean number at Loch Melfort (mean = 3.5). It was not surprising that the greatest barnacle cover was recorded in cages which excluded all snails and the lowest barnacle cover from cages containing *N. lapillus*. The latter treatment recorded an increase in the number of empty barnacle tests. *Littorina littorea* were also found to reduce barnacle cover, inhibiting barnacle settlement (the experiment spanned the 2005 *S. balanoides* recruitment) and/or growth. This inhibition may be indirectly related with *L. littorea* and more directly related with an increase in the observed biofilm which increased with the absence of *L. littorea* in Lochs Fyne and Caolisport. However, regional differences were observed in cover of the biofilm with a greater cover recorded in the Clyde than the west coast and as no significant regional differences were observed in barnacle cover, the influence of *L. littorea* should not be ruled out. Previous studies have found a reduction in barnacle settlement with the removal of *L. littorea* (Bertness 1984; Buschbaum 2000) and have suggested that the observed decline was linked with an increase in the accumulation of sediment. No sediment accumulation was observed in any of the cage treatments throughout the study area during this study.

The effects of grazing of intertidal algae are well known (see Hawkins and Hartnoll 1983 for an in-depth review). It is well known that the exclusion of molluscan grazers from the intertidal will lead to an increase in algal biomass and abundance of micrograzers (Menge 2000). Many studies have examined the effects of *L. littorea* on intertidal algal communities (for examples see Lubchenco 1978; Bertness 1984;

Albrecht 1998; Buschbaum 2000; Jenkins *et al.* 2005). These studies recorded a rapid increase, with the removal of *L. littorea*, in foliose green algae (e.g. *Enteromorpha* and *Ulva* species) which persisted for several months. *Littorina littorea* has been shown to have a high preference for both *Enteromorpha* and *Ulva* species and only a low preference for brown algae such as *Fucus* and *Ascophyllum* species (Lubchenco 1978). These fucoid species have been shown to be regulated by *Patella vulgata* (L., 1758) as a fucoid canopy, consisting mainly of *Fucus vesiculosus* L., 1753, was established following the initial colonisation of green algae (Southward 1978; Jenkins *et al.* 2005). This initial colonisation was found to develop within two months from excluding limpets (Jenkins *et al.* 2005) and after ten days from the removal of *L. littorea* nearly all exposed surfaces were covered with emergent green algal fronds <3 mm in length at Rhode Island (Bertness 1984) and, in contrast to these studies, no green algae was noted in any treatment throughout the study area of the present study. However, Hawkins (1981) noted that the sequence of colonisation due to limpet exclusions was season dependant. He noted that if limpets were removed in autumn or summer, there was a lack of green algae colonisation which was found to be present when limpets were removed in winter and spring. The only sites where macroalgae were recorded within treatment cages were at Loch Caolisport where *F. vesiculosus* germlings were recorded one month from the start of the experiment. As sites were only visited on a monthly basis, it is conceivable that an initial colonisation of green algae occurred at Loch Caolisport on a much shorter time scale than those recorded in previous studies. In contrast, Lochs Fyne, Long, and Melfort showed no macroalgal growth within treatments suggesting algal colonisation in the absence of grazers occurred at a slower rate. A study examining littorinid grazing in controlling the algal cover on shores of the Swedish west coast found no significant role of grazing with the authors noting that the cages did not exclude all small individuals of *Littorina saxatilis* (Olivi, 1792)

(Lindegarth *et al.* 2001). A similar situation occurred in the present study but was only noted at Loch Long where a maximum of two individual *L. saxatilis* were removed from some, but not all, of the treatment cages and was not found consistently within cages.

Nucella lapillus is a major predator of barnacles (for example see Rangeley and Thomas 1988; Palmer 1990) and mussels (Hunt and Scheibling 2001a) in the intertidal with predation rates found to be stronger in areas of high chlorophyll *a* concentration (Menge 2003) and where abundance of mussels and barnacles were greater (Menge 2000). This study did not show any differences in the predation of barnacles by *N. lapillus* between regions of high and low pelagic primary productivity. However, a regional difference was recorded for predation on *M. edulis* with more mussels found to be preyed on at sites on the west coast which contradicted the findings of Menge (2003). Mussels were found to be more abundant in the Clyde than the west coast (see sections 2.3.1 and 2.3.2.2) and so the dominant prey of *N. lapillus* on the west coast would be barnacles. A change in diet may explain the contradiction in findings with the foraging behaviour of individual *N. lapillus* found to vary considerably (Burrows and Hughes 1991). Although *N. lapillus* are capable of consuming mussels as large as 22 mm SL (Hunt and Scheibling 1998b), mussels support less growth than large barnacles (Palmer 1983; Moran *et al.* 1984; Burrows and Hughes 1990) which may explain why predation rates of *M. edulis* were found to be lower in the Clyde which contained larger *S. balanoides* than the west coast (see section 2.3.4). After feeding on *M. edulis*, *N. lapillus* was found to take a post-ingestive pause but was not found to be necessary when feeding on barnacles which could be sustained over longer periods of time (Burrows and Hughes 1991). Although large mussels would supply a higher caloric value to the predator, they may also increase the chance of the predator, particularly *N. lapillus*, from becoming

ensnared by the byssi of the mussel (Petraitis 1987). The results from this study show that large mussels were only preyed on at Loch Caolisport with small mussels taken from Lochs Fyne, Long, and Melfort (Figure 4.12). This size-dependent predation would imply that the *Nucella* at Lochs Fyne, Long, and Melfort are experienced in mussel predation by reducing the risk of entrapment by byssi of large mussels as described by Petraitis (1987). As mentioned previously, whelk feeding is not continuous (see Palmer 1983; and Burrows and Hughes 1991) but has been found to account for the loss of 5 701 mussels m^{-2} (equivalent to 51% of mussels) on emergent rock (Hunt and Scheibling 1998b) with only one or two large mussels per snail consumed over a period of 30 days (Palmer 1983). The present study only ran for three months which would account for the low overall number of mussels consumed (14.4% of the total). Ideally this study would be run over a prolonged period of time and in parallel with the study carried out in Chapter 2.

This study has shown that predation and grazing effects of *N. lapillus* and *L. littorea* differ between regions but that differences, particularly in grazing pressures, may act at different temporal scales. For this reason, it would be necessary to extend the length of the study but at the same time sample the treatments more frequently, especially at Loch Caolisport, in order to determine the succession of algae and whether the observed cover of *F. vesiculosus* was due to grazer exclusion, a natural settlement, or a combination of the two. Barnacle cover was shown to be affected by both *Nucella* and *Littorina* although the latter may have been an indirect affect due to the biofilm cover which showed an increase in the Clyde. Predation rates of mussels were found to be greater on the west coast which was most probably due to a change in diet from barnacles to mussels. This should be investigated further incorporating in a transplant-type experimental design which would control for regional as well as food variation.

Chapter 5 Wave exposure as a determinant in *M. edulis* spatial variation

5.1 Introduction

Variation in intertidal assemblages, on a large scale (among shores), has been attributed to broad-scale biogeographic changes in species availability (Bustamante and Branch 1996b) or variable environmental factors and wave exposure (Menge 1976) with many species showing a change in their exposure tolerance with latitude. Wave action is usually referred to as exposure although in reality exposure has many other facets (Thomas 1986). The problems associated with the direct measurement of indices of wave action have led authors to propose biologically defined exposure scales (see Ballantine 1961; Moyse and Nelson-Smith 1963; Menge 2003). Previous chapters have examined intertidal community structure, growth rates, and predation and grazing effects in intertidal habitats at sites of similar wave exposure and latitude. In order to separate large- from small-scale influences in distribution, the blue mussel, *Mytilus edulis* (L., 1758), was sampled at sites of varying wave exposures throughout western Scotland.

Mytilus edulis is common throughout the British Isles ranging from the high intertidal down to the shallow subtidal. In their natural habitat, recently settled *Mytilus* species are usually associated with filamentous substrata (primarily macroalgal holdfasts) or small crevices and depressions although their settlement behaviour appears to vary considerably among populations (Hunt and Scheibling 1996). Colonisation of empty space by *M. edulis* can occur in two different ways; by lateral movement of juvenile or adult mussels (Gilek *et al.* 2001) or by recruitment from the water column as primary settlement (Bayne 1964), which increases if the surface is irregular or fibrous (Seed 1976; Gilek *et al.* 2001). Primary settlement is likely to depend on large scale

oceanographic and environmental processes such as oceanic currents, the direction of the prevailing wind, and the intensity of exposure to waves.

Waves impinging at any point on a marine shore may be either the result of relatively local wind action or may arrive as swells from more distant weather systems and although wave refraction alters the direction of waves along shorelines, waves will only have a pronounced effect on shores that face into the waves (for examples see Denny 1985; Denny *et al.* 1985; Thomas 1986; Denny 1987, 1995). In particular a shore will be affected by waves in proportion to the angle through which it is open to the sea, its aspect relative to the range of wind directions, and the distribution of shallow water within the fetch. Wave action impacts strongly on the low to mid shore community structure and causes the development of radically different assemblages on a scale of tens of metres (Bustamante *et al.* 1997). Disturbance by wave-generated hydrodynamic forces is important in determining the structure and dynamics of communities on many wave-exposed shores (e.g. Dayton 1971; Menge 1976; Sousa 1979; Paine and Levin 1981; Hunt and Scheibling 2001b).

Wave exposure has been widely accepted as being one of the most important factors determining the distribution and abundance, both spatially and temporally, of intertidal organisms (Jones and Demetropoulos 1968; Harger 1970; Denny 1987; Alvarado and Castilla 1996). Exposure and wave action have been found to affect mussel size, growth, and biomass (see McQuaid and Lindsay 2000) which, in some cases, have been found to be species and site specific. Smaller *M. edulis* were found at more wave exposed locations in southern California (Harger 1970) which may be due to the attachment strength decreasing with an increase in mussel size (Hunt and Scheibling 1998a, 2001a). However, the opposite was found in South Africa for the mussel, *Perna perna* (L., 1758) (McQuaid and Lindsay 2000) and for *M. edulis* in Wales (Jones and

Demetropoulos 1968), where large individuals were found on more exposed shores and no effect of wave action was found on mussel size in southern California for *Mytilus californianus* (Conrad, 1837) (Harger 1970). Mussel size was also found to be dependent on where the individual mussel was situated within the mussel bed. Those near the edge of the bed were observed to be larger than those in the centre (Dolmer 1998).

Growth performance and population density are likely to respond independently to wave action through seperate effects on food availability and recruitment/wave-induced mortality respectively (McQuaid and Lindsay 2000). *Perna perna*, in South Africa, had faster growth rates at exposed shores than sheltered shores (McQuaid and Lindsay 2000). The authors showed that both site and initial length had significant effects on growth with mussels having a higher growth performance and reaching their maximum theoretical length at exposed sites. Mussels were found to be larger on exposed shores because their much faster growth offset the higher mortality rates and lower longevity (McQuaid and Lindsay 2000).

Both filter-feeder and total animal biomass were found to be significantly higher on exposed rather than sheltered shores (Bustamante and Branch 1996a; Bustamante *et al.* 1997; McQuaid and Lindsay 2000) which may indicate the importance of energy subsidies into the system through wave action (McQuaid and Lindsay 2000). A possible explanation for a high biomass of filter-feeders on exposed shores include a higher concentration of particulate food, or a higher water turnover that will replenish food more rapidly than on sheltered shores (Bustamante and Branch 1996b). However, the authors pointed out that other factors, such as biotic interactions and physical disturbance, may also influence biomass. As with mussel size, body weight of *M.*

edulis was also found to have an inverse relationship with wave force (Harger 1970) suggesting a possible site specific interaction.

As discussed previously (see above), wave exposure is a major environmental factor influencing intertidal communities. The effect of wave exposure on intertidal mussels, however, has been found to be both species and site specific. Identifying regional patterns, as a result of food supply and oceanography, and being able to separate them from local variation such as wave exposure, is necessary in order to understand the distribution of *M. edulis*. Previous chapters, which examined sites of similar wave exposure, suggest that mussels in the Clyde will be of a larger size, with potentially a higher biomass, than those on the west coast due to the increased pelagic primary productivity found within the Clyde area and its effect on rates of growth and mortality, carrying capacity, and recruitment. Differences in the mussel populations among sites of similar wave exposure outside the Clyde may be expected to show latitudinal variation. From examining the literature it would be hard to predict what effect wave exposure would have on mussels along the Scottish west coast as conflicting results from previous studies (e.g. Jones and Demetropoulos (1968) in Wales versus Harger (1970) in California) make prediction of the effects of wave action difficult. Although it is clear that differences will occur between sheltered and exposed sites. The main null hypothesis to be tested was:

H_0: Shell length, biomass, and percent cover of the mussel, *M. edulis*, are homogenous throughout the study area and wave exposure gradients.

In order to test the null hypothesis, a wave exposure index was calculated for the west coast of Scotland taking into account the fetch of the area and average wind speed. Mussels were sampled throughout western Scotland at differing wave exposures and analysed using an image analysis package.

5.2 Materials and Methods

In July 2003, 55 rocky shores were visited along the Scottish west coast from Southend on the Mull of Kintyre in the south to Skullomie, Kyle of Tongue in the north (Figure 5.1, Appendix 5.1). Shore profiles were taken at each site from the water's edge to the top of the littoral fringe recording distance up the shore with every 0.5 m height interval. Two shore heights corresponding to mean high water neaps (MHWN) and mean low water neaps (MLWN) were established (see section 2.2.2 for an in-depth description). At each shore height, four 50×50 cm quadrats, each containing a smaller 10×10 cm quadrat, were photographed with a Ricoh Caplio RR30 digital camera (2048 normal picture quality) for estimation of mussel cover. Any mussels within the smaller quadrat were removed, placed in a labelled bag, and frozen for later analysis. The location of each shore was recorded using a Garmin GPS 76 with all study sites divided up into four areas (Figure 5.1).

5.2.1 Calculation of a wave exposure index for western Scotland

Wave exposure was calculated along the Scottish west coast (Figure 5.1 to Figure 5.5) based on modified techniques used by Thomas (1986) and Burrows (unpublished). The coastline was divided into 0.5 km grid cells with an exposure value calculated for each cell. The relevant wind rose for each cell was divided into 16 sectors of 22.5°. The sum of the product of the fetch, square of the average wind speed, and the proportion of time that wind blew within each sector was calculated using data from Tiree for 1993 to 2001. The resultant value was a measure of wave exposure with a range in values of 400 (extremely sheltered) to 39 000 (extremely exposed) expressed as $km.kt^2\ s^{-2}$ where km = kilometres, kt = knots, and s = seconds. Log_{10} values were used in the analysis.

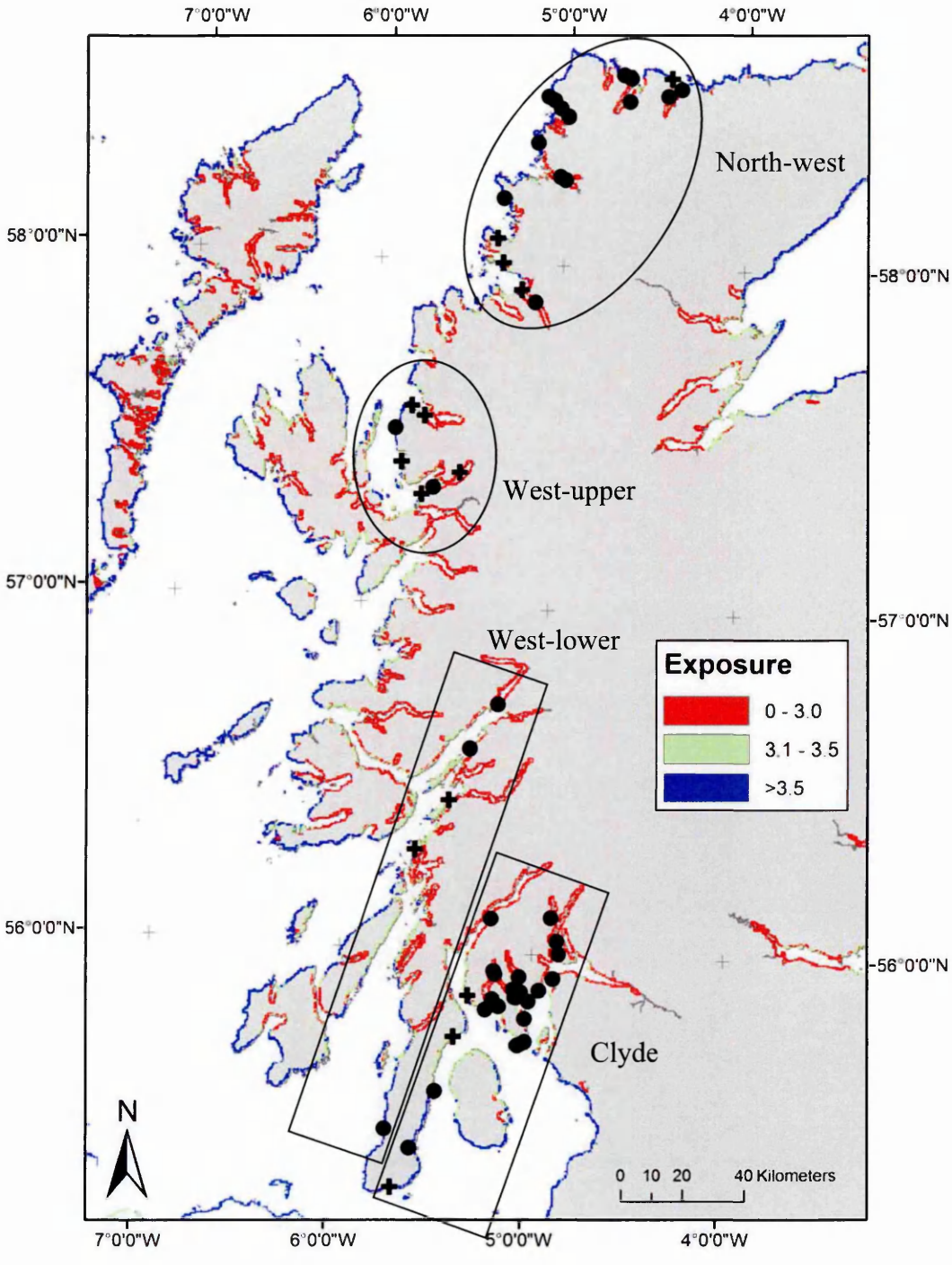


Figure 5.1 Locations of sites around the Scottish west coast which were sampled for mussels in July 2003. Sites where mussels were recorded are denoted by a circle and those where no mussels were found by a +. Three wave exposures are shown with sheltered sites denoted as red and exposed as blue (log_{10} units of $km.kt^2\ s^{-2}$ were used).

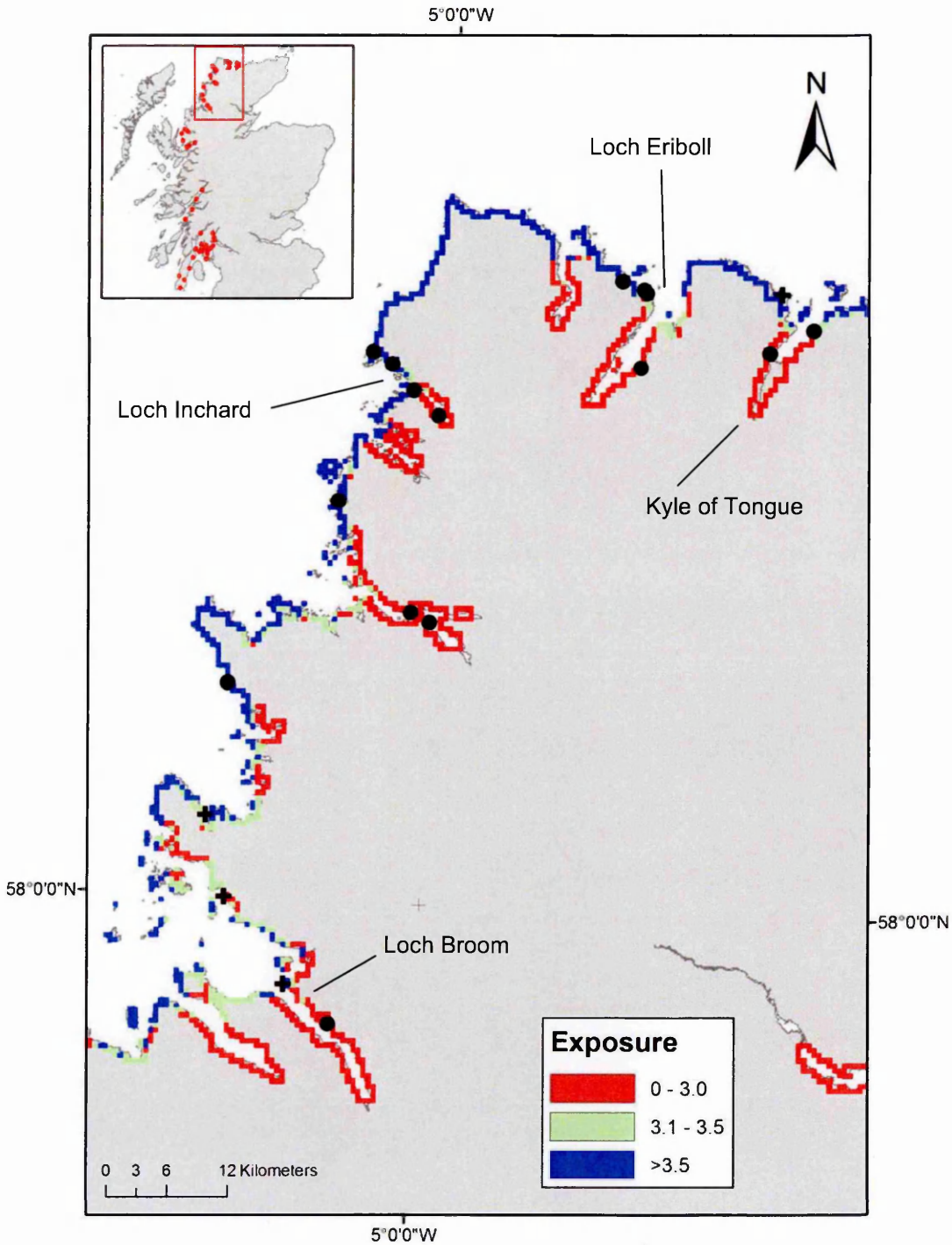


Figure 5.2 North-west area site locations. Sites where mussels were recorded are denoted by a circle and those where no mussels were found by a ✚. Three wave exposures are shown with sheltered sites denoted as red and exposed sites as blue ($\log_{10}$ units of $km.kt^2\ s^{-2}$).

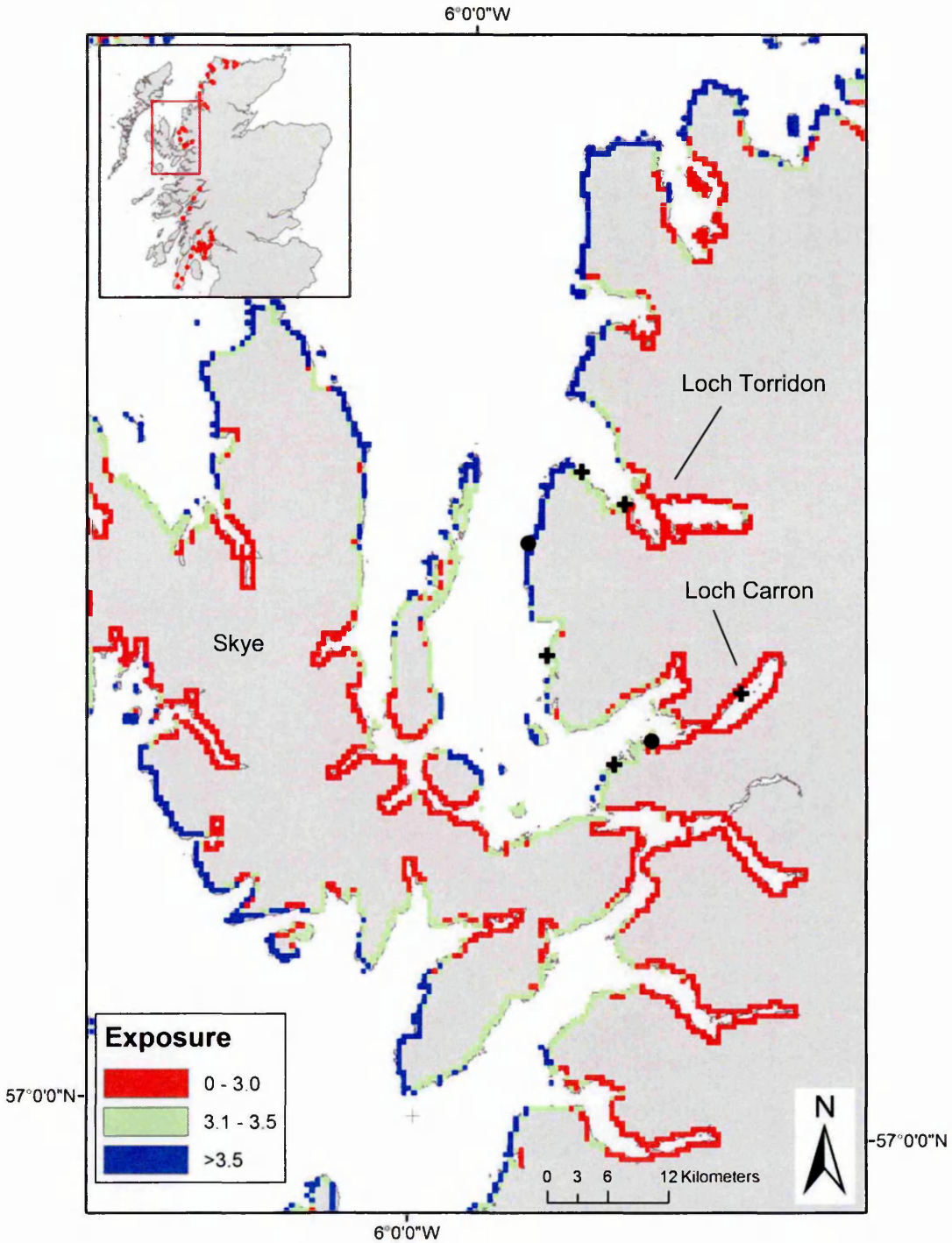


Figure 5.3 West-upper area site locations. Sites where mussels were recorded are denoted by a circle and those where no mussels were found by a ✚. Three wave exposures are shown with sheltered sites denoted as red and exposed sites as blue (log_{10} units of $km.kt^2\ s^{-2}$).

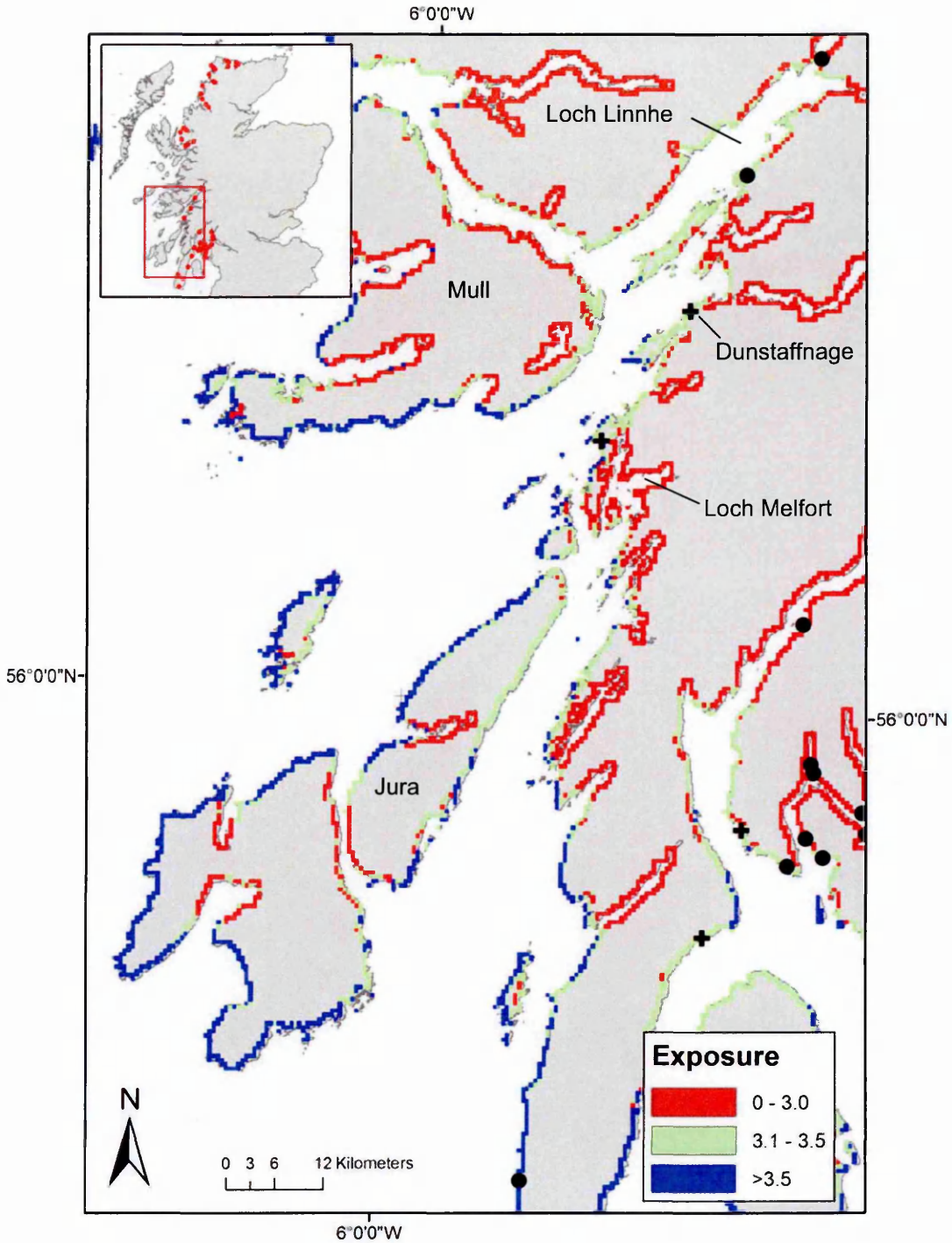


Figure 5.4 West-lower area site locations. Sites where mussels were recorded are denoted by a circle and those where no mussels were found by a ✚. Three wave exposures are shown with sheltered sites denoted as red and exposed sites as blue (log_{10} units of $km.kt^2\ s^{-2}$).

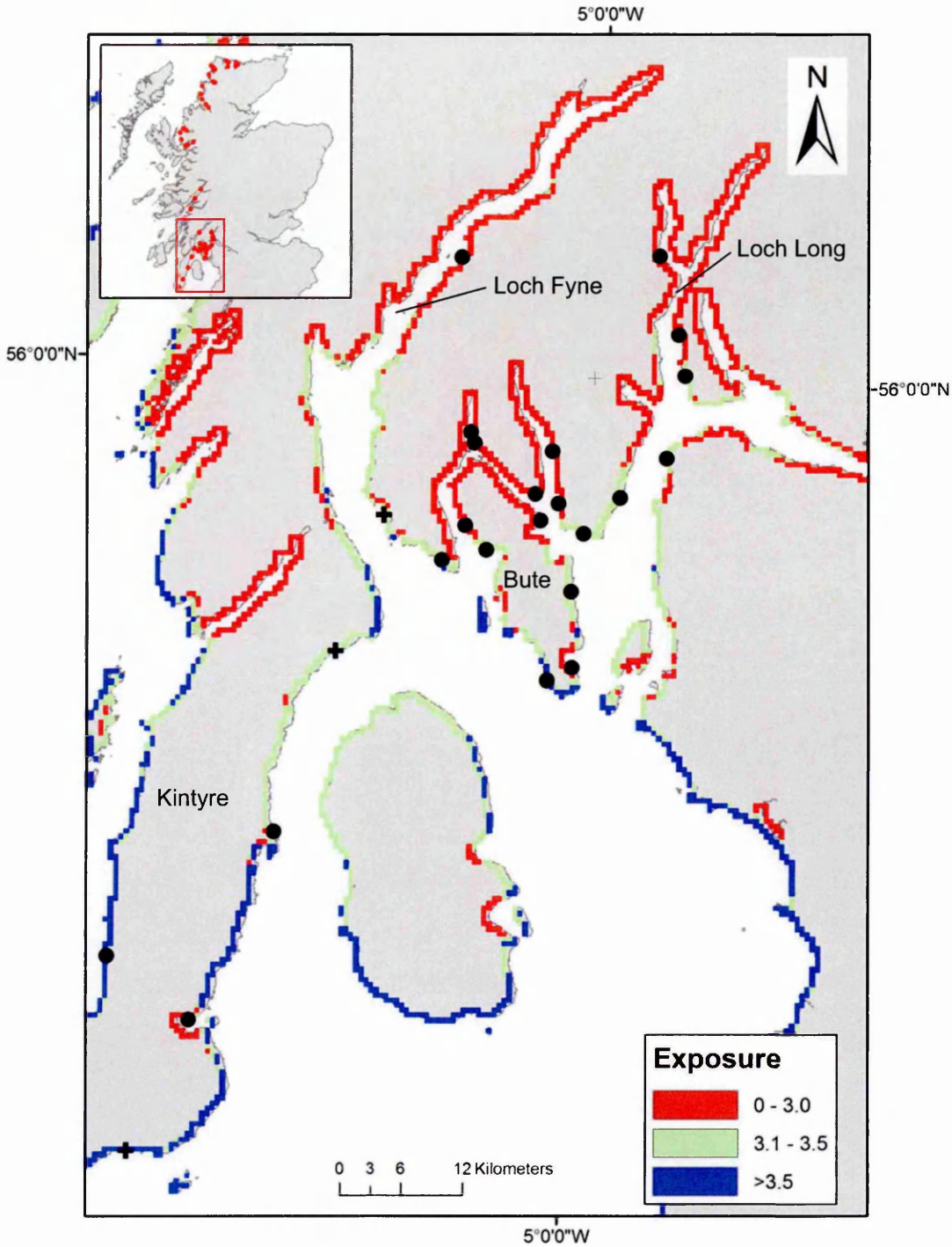


Figure 5.5 Clyde area site locations. Sites where mussels were recorded are denoted by a circle and those where no mussels were found by a ✚. Three wave exposures are shown with sheltered sites denoted as red and exposed as blue (log_{10} units of $km.kt^2\ s^{-2}$).

5.2.2 Sampling and image analysis to determine mussel cover and size distributions

Mussel cover was estimated using the images from the 50×50 cm quadrats, as described previously for estimating barnacle, mussel, and macroalgae cover from 30×30 cm quadrats (section 2.2.4). Mussel size was categorised, by eye, as small or large as shown in Figure 5.6a for large mussels and Figure 5.6b for small mussels.

After thawing, all mussels were separated out and rinsed clean of debris with seawater. Each mussel was evenly spaced on a white background and digitally photographed for later image analysis. Each image contained a label and coin for scale. All four samples from each shore height were combined with a sub-sample taken containing 6 of each 10 mm size class. This sub-sample was labelled, bagged, and frozen for biomass analysis at a later date. Sub-sampled size classes were measured (shell length, depth, and width Figure 3.5) with digital callipers (Moore and Wright digital calliper, ±0.02 mm), dissected, weighed without the shell, and the flesh dried at 60°C to a constant weight.

Mussel lengths were measured using an image analysis program, "Image J" (National Institutes of Health, USA 2005). All photographs were changed to 8-bit with an automatic threshold. The image was edited to separate out any mussels that were found to be touching and before analysis a minimum object size of 40 pixels was set in order to filter out debris. The image analysis program calculated the maximum length of each mussel, and the coin used as a scale, in pixels. These measurements could then be converted to millimetres. Mussel outlines were saved as a separate image file with measurements imported to Excel™ for comparison with wave exposure indices for each individual site (Figure 5.6).

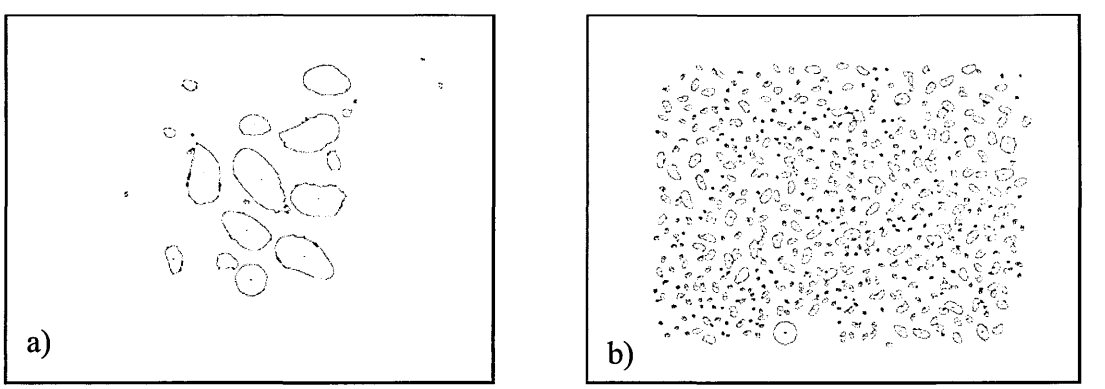


Figure 5.6 *Mytilus edulis* outlines from "Image J" from a) an inner and b) an outer loch site.

5.3 Results

Mytilus edulis were found at 75% of the 55 rocky shores sampled with no mussels found at 14 sites, half of which were in the West-upper and West-lower area (Figure 5.3 and Figure 5.4, respectively). A total of 12 sites were sampled in the combined areas of West-upper and West-lower. No mussels were found in seven of the 12 sampled sites and so these two areas were combined to form one large area, West.

Wave exposure throughout the sampled sites ranged from a sheltered 2.6 km.kt^2 s^{-2} at the mid site of Loch Inchard (North-west) to an exposed 4.1 km.kt^2 s^{-2} at the outer site of Loch Inchard (overall mean exposure of 3.2 km.kt^2 s^{-2}; North-west mean exposure of 3.3 km.kt^2 s^{-2}, n = 19). Sites sampled in the Clyde had a similar range of wave exposures (mean = 3.1 km.kt^2 s^{-2}, range 2.7 to 3.9 km.kt^2 s^{-2}, n = 24) to those in the West area (mean = 3.1 km.kt^2 s^{-2}, range 2.7 to 4.0 km.kt^2 s^{-2}, n = 12) with no significant difference found in wave exposure between areas (One-way ANOVA, $F_{3,51} = 0.95$, P = 0.425). Three categories of wave exposure were defined (sheltered≤3.0; 3.0<intermediate<3.5; and exposed≥3.5, Figure 5.7) although it was not always possible to include an intermediate sample within the analysis. This categorisation of sites by wave exposure, into sheltered and exposed, minimised the orders of magnitude differences between the wave exposure resolution of 0.5 km and the site location. Although the calculated difference between a wave exposed and a wave sheltered site was only 0.5 km.kt^2 s^{-2} on a log scale (see Figure 5.1 to Figure 5.5), this equates to 2 100 km.kt^2 s^{-2}.

Cover of *M. edulis* was not found to differ between the three defined exposure types (Kruskal-Wallis test, H = 1.43, P = 0.490, Figure 5.7) or areas (Kruskal-Wallis test, H = 7.63, P = 0.054, Figure 5.8). No difference was found between the cover of small (<100 mm) and large (≥100 mm) mussels when examining the differences in the slopes of the regressions (ANCOVA, $F_{2,49}$ = 0.35, P = 0.709), mussel size was found to differ significantly with respect to proportional cover at varying wave exposures when a reduced model was fit (ANCOVA, $F_{2,51}$ = 15.78, P<0.001) with small mussels found at sites with a high wave exposure (Figure 5.9).

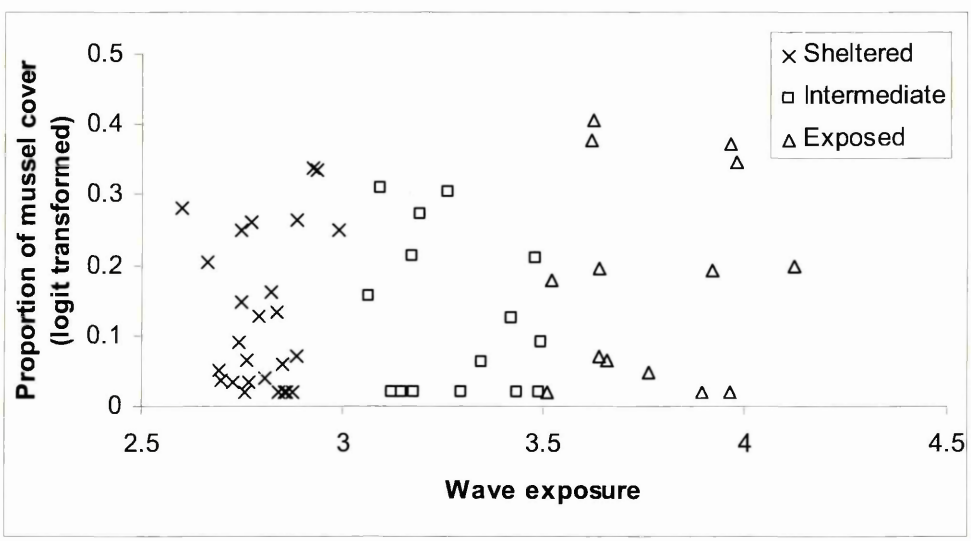


Figure 5.7 Proportional cover of *M. edulis* transformed using the logit function at three differing wave exposures of sheltered, intermediate, and exposed.

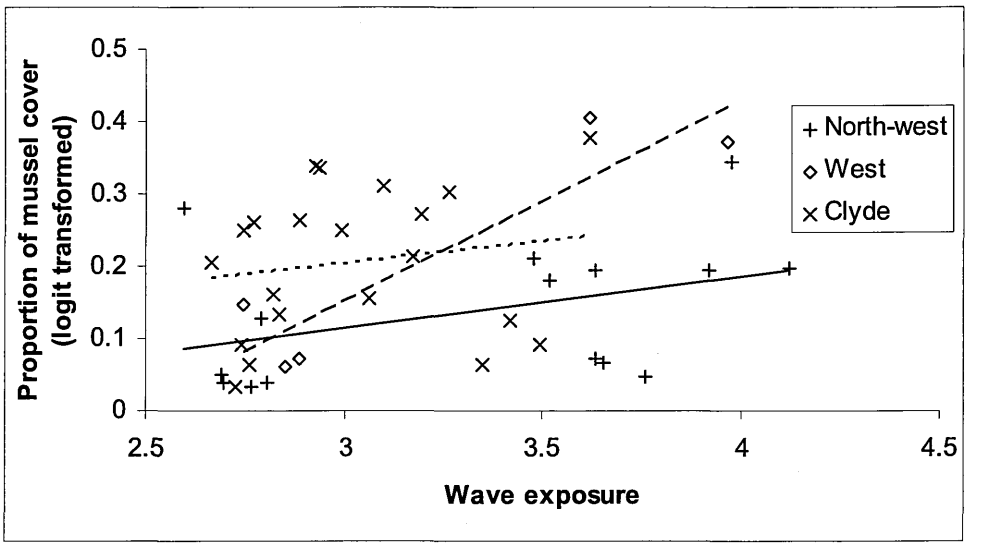


Figure 5.8 Proportional cover of *M. edulis* transformed using the logit function at differing wave exposures at the three areas. North-west (solid line), West (large dashed line), and Clyde (small dashed line) regressions are shown.

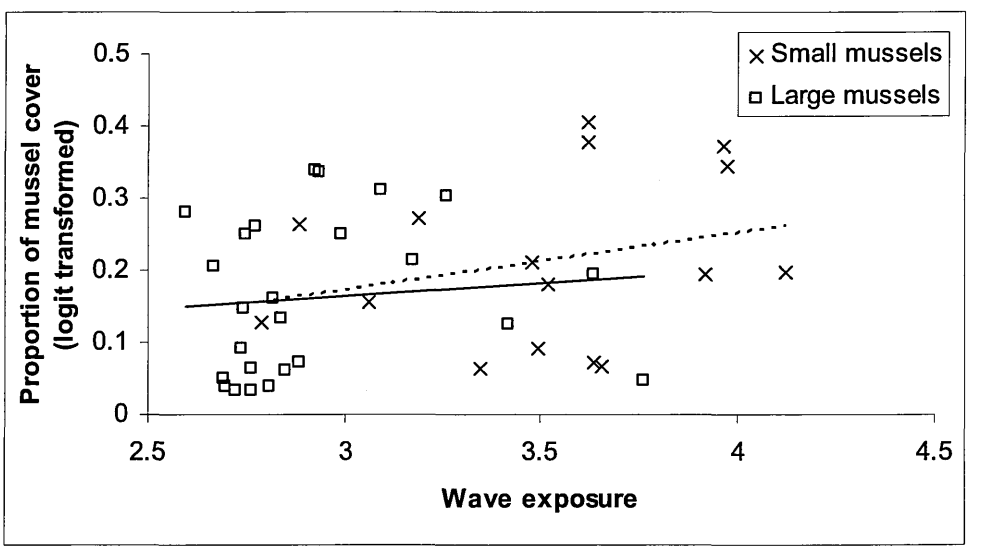


Figure 5.9 Proportional cover, logit transformed, of small (dashed line) and large (solid line) *M. edulis* at differing wave exposures.

5.3.1 Model likelihood of sites being dominated by small or large mussels

Sheltered sites had a higher number of large mussels compared with exposed sites which had a higher number of small mussels (One-way ANOVA, $F_{1,16095} = 1017.99$, $P<0.001$ Figure 5.10). Sheltered sites were found to have a bimodal size frequency distribution with exposed sites found to have a unimodal distribution (Figure 5.10). Mussel size was found to differ significantly with area (One-way ANOVA, $F_{2,16094} = 1311.39$, $P<0.001$, Figure 5.11). Sites within the Clyde had significantly larger mussels compared with those in the West and North-west with the latter having the smallest mussels (Fisher's LSD test).

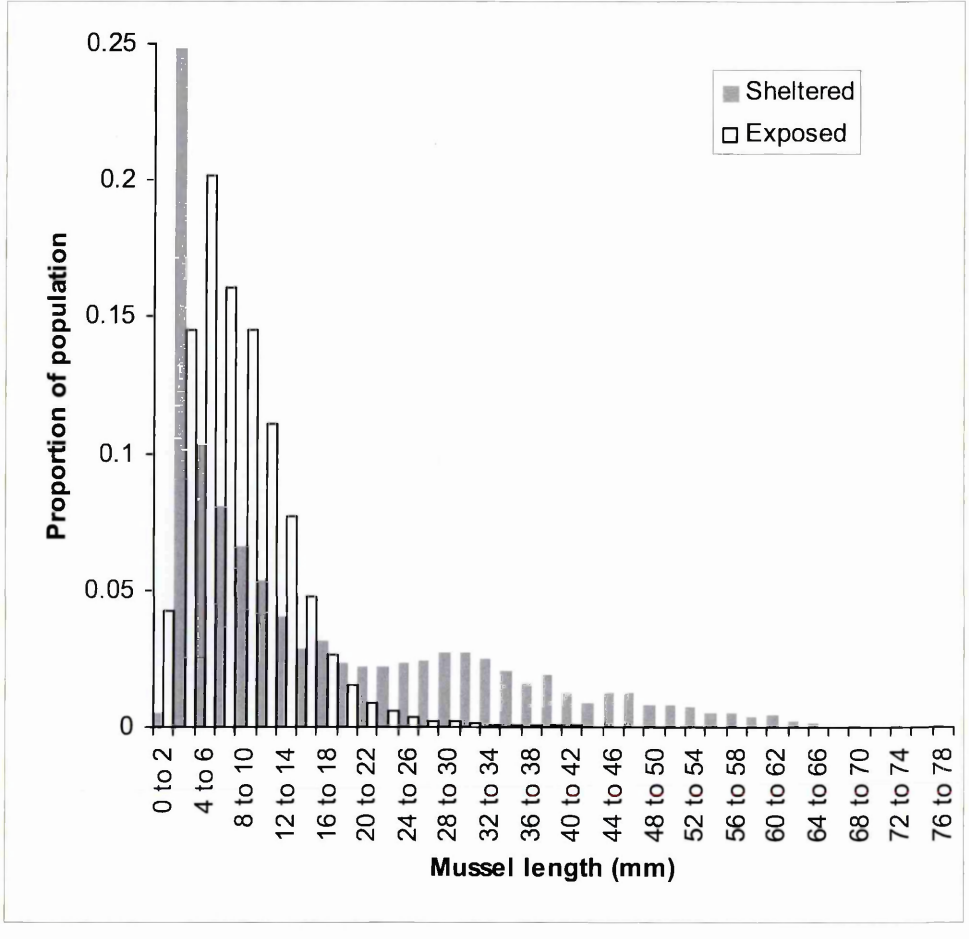


Figure 5.10 *Mytilus edulis* length frequency distribution as a proportion of the population at sheltered and exposed sites.

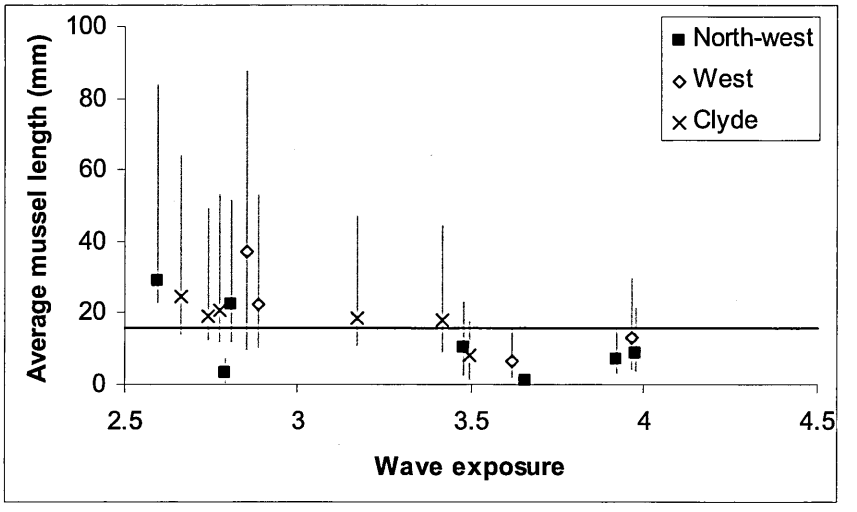


Figure 5.11 Average *M. edulis* length at sites of differing wave exposure within three areas. The horizontal line denotes the overall average length of 15.9 mm with vertical lines linking upper and lower quartiles.

5.3.2 Biomass of *M. edulis* at sites of differing wave exposure

Biomass of *M. edulis* was found to be significantly smaller at exposed sites compared to sheltered sites over the study area (Table 5.1, Figure 5.12). No significant difference in biomass was recorded for either of the remaining factors of area or height, or their respective interactions (Table 5.1).

Table 5.1 Results of the three-way ANOVA examining biomass of *M. edulis* at three different areas, in exposed and sheltered locations, and at upper and lower shore heights.

	d.f.	SS	MS	F ratio	P value
Area	2	613.3	306.6	0.93	0.397
Exposure	1	5139.2	5139.2	15.58	<0.001
Height	1	0.6	0.6	<0.01	0.967
Area×Exposure	2	339.6	169.8	0.51	0.599
Area×Height	2	150.0	75.0	0.23	0.797
Exposure×Height	1	27.2	27.2	0.08	0.774
Residual	177	58380.6	329.8		
Total	186				

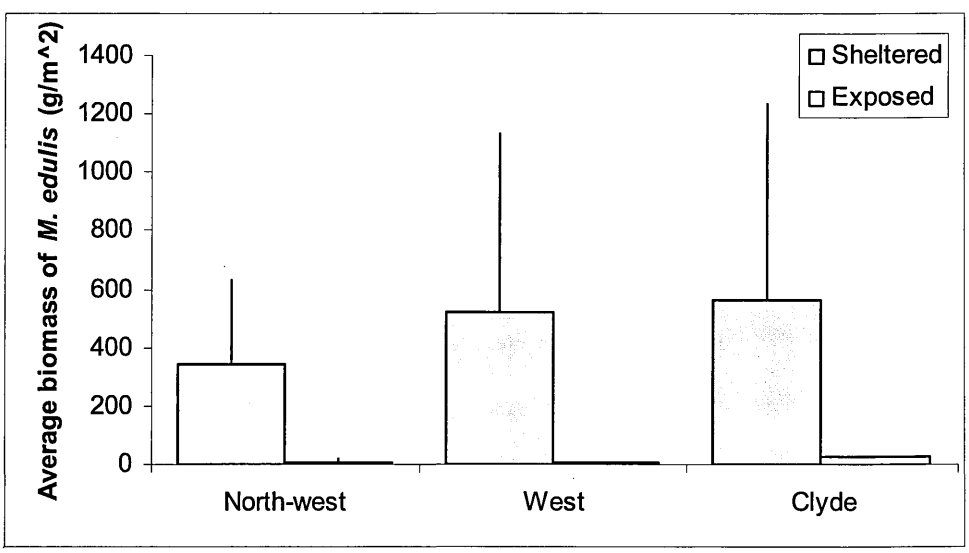


Figure 5.12 Average biomass (gm^{-2} of flesh dry weight) of *M. edulis* at sheltered and exposed sites of the four areas with 95% confidence intervals shown.

A logarithmic relationship was found between flesh dry weight and length of *M. edulis* at the three areas of North-west, West, and Clyde (Figure 5.13, Figure 5.14, and Figure 5.15, respectively). The regressions of sheltered and exposed sites within the North-west area were found to have significantly different slopes (ANCOVA, $F_{1,62} = 29.57$, $P<0.001$). No difference was found between the slopes of the regressions for the West (ANCOVA, $F_{2,47} = 2.69$, $P = 0.078$) and Clyde (ANCOVA, $F_{2,92} = 0.99$, $P = 0.375$) areas. By fitting a reduced model it was possible to determine that sheltered and exposed sites of the West area differed significantly (ANCOVA, $F_{2,49} = 4.47$, $P = 0.016$), as was found in the Clyde (ANCOVA, $F_{2,94} = 4.21$, $P = 0.018$). Mussels at sheltered sites were found to be significantly heavier in all areas.

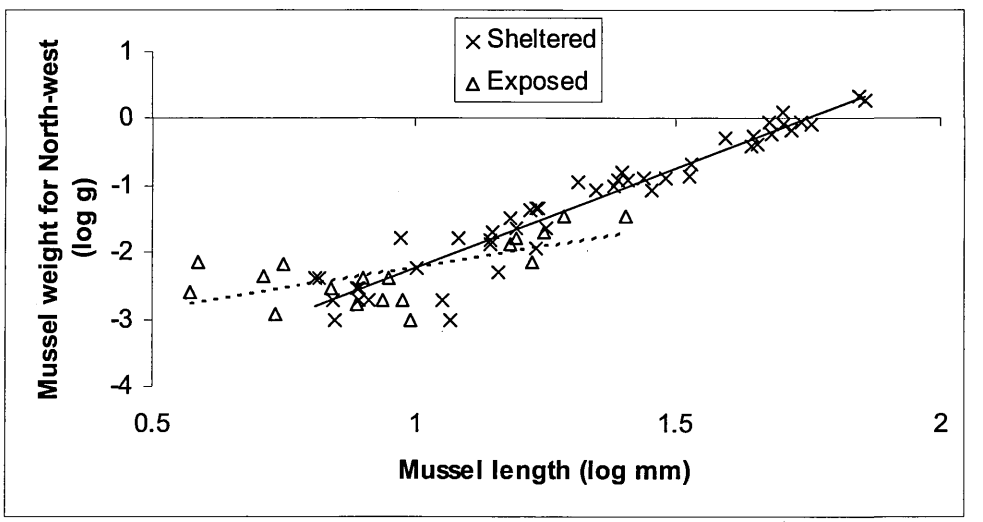


Figure 5.13 Weight-length relationships for *M. edulis* at sheltered (solid line, y = 3.0197x-5.267, $R^2 = 0.926$) and exposed (dashed line, y = 1.2538x-3.4972, $R^2 = 0.4212$) sites in the North-west area.

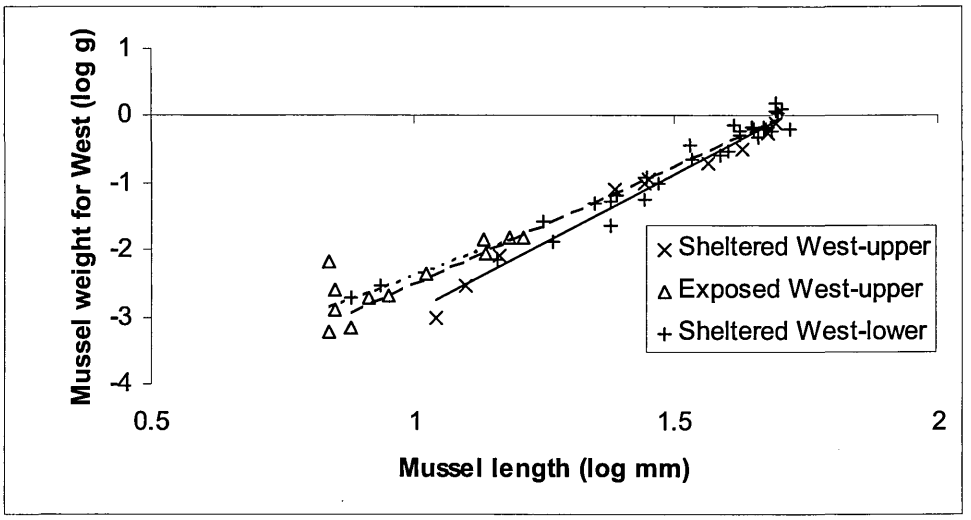


Figure 5.14 Weight-length relationships for *M. edulis* at the West-upper area in sheltered (solid line, y = 4.06x-6.9642, R^2 = 0.975) and exposed (small dashed line, y = 2.9136x-5.3085, R^2 = 0.697) sites and at the West-lower area at sheltered sites (large dashed line, y = 3.5241x-6.0597, R^2 = 0.952).

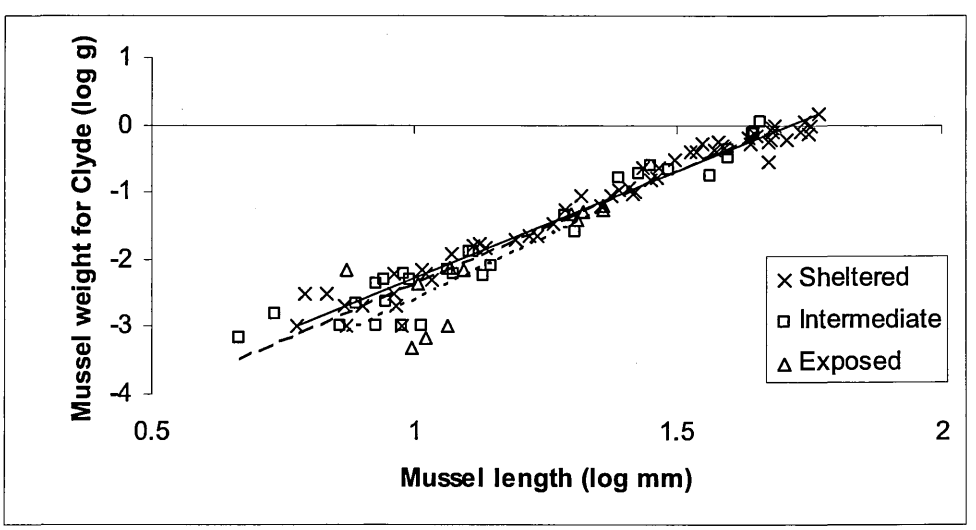


Figure 5.15 Weight-length relationships for *M. edulis* at sheltered (solid line, y = 3.1751x-5.4452, R^2 = 0.966), intermediate (large dashed line, y = 3.3665x-5.7368, R^2 = 0.934), and exposed (small dashed line, y = 3.7153x-6.3268, R^2 = 0.660) sites in the Clyde area.

5.4 Discussion

The blue mussel, *M. edulis*, is one of the major filter-feeding species found along the Scottish west coast throughout the wave exposure gradient. This study has shown populations at wave exposed sites were dominated by small mussels with small biomass per unit area while large mussels with large biomass were found at more wave sheltered sites. As described previously (see section 5.1) variation in mussel size and biomass have been shown to be species and/or site specific with no clear indication as to whether *M. edulis* would be expected to be small or large, in shell length or biomass, at wave exposed versus wave sheltered sites. Filter feeders at a wave exposed site would be exposed to an increased and more turbulent water flow which could potentially benefit the organisms by increasing the supply of suspended food (Griffiths 1980a, 1980b; Camacho *et al.* 1995; Dolmer 1998; McQuaid and Lindsay 2000), reducing predation rates of mobile predators (Robles *et al.* 2001), and reducing intraspecific competition through disturbances leading to patch formation. An increased water flow has been shown to reduce feeding rates in both barnacles (Sebens 1984) and mussels (Sebens 1984; Leonard *et al.* 1998) which would potentially reduce individual growth rates leading to smaller maximum sizes. However, Sanford *et al.* (1994) found the opposite in the barnacle, *S. balanoides*, with an increased number found to feed at increased flow speeds. Increased feeding would ultimately lead to increased size at high flow sites, which was not found during this study of *M. edulis*.

The predominance of smaller individuals on more exposed shores could reflect greater predation on sheltered shores (Menge 1976), or dislodgement of large mussels by waves on exposed shores (Paine and Levin 1981; McQuaid and Lindsay 2000) although an abundance of *Nucella lapillus* (L., 1758) on dense beds of small *Mytilus* at exposed sites

suggested a possible predation pressure as a size related mortality from dislodgement (Kitching *et al.* 1959). A study examining *Mytilus galloprovincialis* (Lamarck, 1819) in South Africa found significant relationships between wave exposure and; mussel cover, mean length, and biomass with peaks found at intermediate exposures rather than at extremes (Hammond and Griffiths 2004). Their results show similar values of mussel biomass and length for sheltered and exposed shores and only mussel cover showed distinct differences between the exposures. These results suggest that *M. galloprovincialis* is not adapted in coping with the extremes of the range of wave exposure (sheltered and exposed) but this was not found to be the case for *M. edulis* on the west coast of Scotland. Although few comparisons were carried out involving intermediate exposures (see Figure 5.15), distinct differences were observed between the extremes in both mussel length and biomass at all areas which showed a negative relationship with increasing exposure, rather than a polynomial relationship as described by Hammond and Griffiths (2004), while the percentage cover of mussels remained constant over the exposure gradient (Figure 5.7).

The results of the present study showed a bimodal length frequency distribution at sheltered sites and a unimodal distribution at exposed sites (Figure 5.10). Bimodal size frequency distributions in mussels have been previously observed throughout the exposure gradient (see Alvarado and Castilla 1996). The authors suggested that the first mode in the size distribution of the mussel would arise due to the permanent presence of a large number of recruits in the environment accompanied by a high mortality rate of small individuals with the second mode resulting from a process in which mortality decreases with increasing mussel size. The second mode at all three exposures (sheltered, semi-exposed, and exposed) was found to occur at a larger size at sheltered sites with the initial mode occurring at the same size throughout the exposure gradient

(Alvarado and Castilla 1996). Although *M. edulis* at sheltered sites on the west coast showed a bimodal distribution, the initial mode peaked at a smaller size than the corresponding peak from exposed sites. If mussels at exposed sites were size limited due to increased mechanical forces of wave action leading to increased mortality, a second mode would not be expected since the mussel population would not reach the critical size in which mortality would decrease.

As well as the mechanical affects of waves on mussel mortality, predation also plays a significant role (Menge and Farrell 1989) but was not found to be an important source of variation in patch area (Hunt and Scheibling 2001a) which was most probably due to physical disturbances. Predation rates of *N. lapillus* on *M. edulis* at sites of similar wave exposure were discussed previously with more smaller mussels preyed on than large ones (see Chapter 4). This supported the theory of increased predation pressure at sheltered sites, as described by Menge (1976), resulting in larger individuals found at sheltered sites. Variation in predation rates on *M. edulis* by *N. lapillus* at sites of differing wave exposure were not examined. Due to the increased risk of *N. lapillus* becoming dislodged at sites of high wave exposure, a reduction in foraging time (i.e. predation rate) would be expected. For this reason, it does not seem likely that predation by *N. lapillus* plays a significant role in structuring *M. edulis* communities at sites of high wave exposure.

Mussel size was not found to differ between regions at sites of similar wave exposure suggesting that large scale variation in pelagic primary production did not have a significant effect on mussel size as was expected. Variation in local conditions, such as water flow rates, wave exposure, or sea surface temperature, may have a greater effect on mussel size. Average sea surface temperatures in the Clyde are higher, by

approximately 1°C, than those of the North-west during summer (June to August) and autumn (September to November) with temperatures in the Clyde becoming more similar to those of the North-west during winter (December to February) months (Anonymous 2003, 2005). Water temperature at an offshore location off California was not found to affect *M. edulis* growth rates (Page and Hubbard 1987).

Pelagic primary production has been shown to be higher in the Clyde compared with the west coast (see Figure 1.1 to Figure 1.3) so it would not be entirely surprising to find larger mussels in the Clyde which has a higher concentration of suspended food. Previous results (Chapter 3) have shown that mussels in the Clyde did not grow faster than those on the west coast so the effects of enhanced primary productivity were not evident in regional differences which would be consistent with Figure 5.11. The coastline of the Scottish west coast is extremely complex with many fjordic-like inlets and embayments leading to smaller scale variation in food availability. It has been estimated that mussels could potentially filter 65 m^3m^{-2} per tidal immersion period, reducing the phytoplankton population immediately above the mussel bed (Archambault *et al.* 1999). Large embayments, such as sea lochs, which have a low surface-area to volume ratio and large retention time, may allow mussel by-products, which may increase primary production of local phytoplankton populations (Archambault *et al.* 1999), to accumulate within the embayment. This may allow the rate of primary production of phytoplankton within large embayments to increase above the grazing rate imposed by the mussels, thereby increasing the concentration of chlorophyll *a* in bays relative to offshore areas with mussel shell length and body mass increments found to be generally higher inside the embayment than outside (Dowd 1997; Archambault *et al.* 1999). This positive feedback mechanism combined with a wave sheltered

environment would lead to increased growth to a greater maximum size and biomass with space, and ultimately intraspecific competition, being the major limiting factors.

This study has shown that *M. edulis* shell length and biomass decline with increasing wave exposure throughout western Scotland. These differences were evident at large spatial scales but no work was carried out in order to examine smaller, local variation, variation in predation rates at sites of varying wave exposure, recruitment variation, and influences from freshwater runoff (see Chapter 6). Previous work carried out (Chapter 2) demonstrated the major influencing factor when examining species abundance to be site specific rather than the larger scale of region which emphasises the need, when examining organisms over large spatial scales, to include smaller scale processes into the analysis. Although not discussed in the present study, water flow rates have been shown to significantly influence mussel feeding capability and growth rates (Leonard *et al.* 1998) and recruitment of *M. californianus* has been shown to increase with increasing wave exposure (Robles *et al.* 2001). A high recruitment at exposed sites dominated with small mussels would imply a high population turnover assuming maximum mussel size was determined by the mechanical nature of the increased wave action. It is clear from this study that further work would have to be carried out in order to determine variation in recruitment rates, predation pressures, and the significance of the positive feedback mechanism reported for mussels in semi-enclosed embayments such as sea lochs.

Chapter 6 A pilot study examining small to large scale variation of mussel stable isotopes: potential effects of local and regional influences.

6.1 Introduction

Stable isotope analysis is an increasingly useful and powerful tool used in ecological studies in a wide range of environments. Isotope ratios offer advantages over traditional methods including gut content analysis which may pose problems such as the size of the food source, digestion time and identification of the prey, and stomach evertion of the predator to determine trophic positions of species and construct food webs. Stable carbon isotopes provide a more direct means of tracing carbon flow through aquatic food webs, one that has proven especially useful in identifying the plant carbon sources of organisms at higher trophic levels (Fry and Sherr 1984; Araujo-Lima *et al.* 1986; Forsberg *et al.* 1993). The stable isotope ratios in the tissues of consumer species integrate carbon sources over a long time period, and more importantly, can measure what is actually assimilated into body tissue. Typically, natural abundances of isotopes of carbon and nitrogen are used, and the measurement of both concurrently yields more information on feeding relationships than either element alone (Grey *et al.* 2002).

6.1.1 Using carbon to discriminate between plant sources

Once carbon is fixed as organic matter in autotrophs, the isotope ratio is passed on to consumers with only slight enrichment, an increase in $\delta^{13}C$ (a change in $^{13}C/^{12}C$ relative to a reference material) of <1‰, in the heavier isotope (^{13}C) at each trophic transfer (Rounick and Hicks 1985; Forsberg *et al.* 1993; France 1995; Jacob *et al.* 2005). The $\delta^{13}C$ signature of an organism reflects the isotopic composition of the diet and provides information on the source of carbon to the food web (Grey *et al.* 2002). When there are relatively few isotopically distinct plant groups, it is often possible to determine the

plant carbon source(s) of an animal directly from its carbon isotope ratio as their signatures pass relatively unchanged between trophic levels (Forsberg *et al.* 1993; Leite *et al.* 2002). During photosynthesis, the relative proportions of carbon isotopes incorporated into plant tissues depends on whether plants use C_3, C_4, or Crassulacean Acid Metabolism (CAM) photosynthetic pathways (Forsberg *et al.* 1993; James *et al.* 2000). Terrestrial C_3 plants have $\delta^{13}C$ values ranging from approximately -32 to -20‰ (mean -27‰) with C_4 and CAM plant $\delta^{13}C$ values ranging from -17 to -9‰ (mean -13‰) (Rounick *et al.* 1982; Boutton 1991). The large range in $\delta^{13}C$ values for terrestrial production makes it hard to distinguish them from aquatic production (Post 2002). Due to a higher selectivity for the lighter isotope during carbon fixation, C_3 plants are significantly enriched in ^{12}C (Forsberg *et al.* 1993) with the $^{13}C/^{12}C$ ratios of terrestrial plants found to be distinct from those of aquatic algae (Rau 1980). Photosynthesis in the marine environment occurs via the C_3 pathway although the $\delta^{13}C$ values of marine and terrestrial C_3 plants do not always resemble one another (Boutton 1991; Leite *et al.* 2002). In lakes, $\delta^{13}C$ is useful for differentiating between two major sources of available carbon, littoral (near shore) production from attached algae and pelagic (open water) production from phytoplankton (France 1995). It is possible to make this distinction due to the fact that the littoral food web tends to be enriched in ^{13}C (less negative $\delta^{13}C$) relative to the base of the pelagic food web. Macroalgae has a wide range of $\delta^{13}C$ values from -8 to -27‰ (mean -15‰) with similar large ranges found in temperate marine phytoplankton (-18 to -24‰), and river-estuarine phytoplankton (-24 to -30‰) (for a review see Fry and Sherr 1984; and Boutton 1991). Although the range of $\delta^{13}C$ values of phytoplankton is large, they are typically near -22‰ which have been shown to be slightly lower (-27‰) at higher latitudes (Boutton 1991).

6.1.2 The role of nitrogen in determining trophic position within food webs

Nitrogen isotopes are less useful in discriminating between plant sources, but since they change consistently through the food web, they can be used to evaluate the consumer's trophic level (Leite *et al.* 2002; Post 2002). The evaluation of the trophic position by nitrogen isotopes makes no diet assumptions, but depends on a proper estimation of plant $\delta^{15}N$ and on the isotopic fractionation constant (Leite *et al.* 2002). On average $\delta^{15}N$ increases by 3‰ from one trophic level to the next (Peterson and Fry 1987; Pinnegar and Polunin 1999; Jacob *et al.* 2005).

6.1.3 Mussels

Mussels have a high biomass within the intertidal and are preyed on by many species (e.g. dogwhelks, crabs, fish, and birds) and so occupy an important position at the consumer base of many marine and aquatic food webs. For this reason, these consumers can provide an appropriate baseline to quantify higher trophic positions (Post 2002) as they are long-term integrators of $\delta^{15}N$ from their diet (McKinney *et al.* 2001). When carrying out carbon and nitrogen isotope analysis on bivalves, it is possible to use either the shell or parts of the soft tissue, each deriving differing results as the shell is greatly influenced by the inorganic carbon (McConnaughey *et al.* 1997) and soft tissue by organic carbon (Post 2002).

6.1.4 Shells

The shell of gastropods and bivalves is a biologically mediated, carbon-based precipitate that reflects the isotopic signature of the inorganic environment (McConnaughey *et al.* 1997). Bivalve shell material records the isotopic composition of the integrated dissolved inorganic carbon (DIC) signal (McConnaughey *et al.* 1997), and the DIC isotopes especially reflect contributions of respiratory CO_2 associated with groundwater inputs and river respiration (Rau 1978; Kline *et al.* 1990; Quay *et al.* 1995; Fry and Allen 2003). The shell material sampled as a proxy for DIC integrates isotopic signals over long time periods, and this integration averages out and minimizes seasonal changes in alkalinity (Bryan *et al.* 1992).

6.1.5 Tissues

Mussel soft tissue reflects the isotopic signature of their diet (Post 2002) and although tissue $\delta^{13}C$ values have been found to generally parallel changes in shell $\delta^{13}C$ (tissue $\delta^{13}C = 0.9\times[\text{shell } \delta^{13}C]-20.5$, $r^2 = 0.84$, $n = 8$) (Fry and Allen 2003), this correlation was much less pronounced in seasonal collections where there was 2‰ seasonal change in tissue carbon isotope values, but <0.5‰ change in shell isotope values (Fry and Allen 2003).

Previous studies on isotope ratios in mussels have mainly focused on animals in freshwater lakes (Rau 1978; France 1995; James *et al.* 2000; Grey *et al.* 2001; Grey *et al.* 2002), rivers (Rounick *et al.* 1982; Forsberg *et al.* 1993; Fry and Allen 2003; Howard *et al.* 2005), and estuaries (Murphy and Abrajano 1994; Yelenik *et al.* 1996;

Keough *et al.* 1998; McClelland and Valiela 1998). Few studies have investigated stable isotopes in the blue mussel, *Mytilus edulis* (L., 1758), in the marine environment (see Wiedemeyer and Schwamborn 1996; Kwak and Zedler 1997; Riera *et al.* 2002). A number of studies have been conducted using stable isotopes in the marine intertidal on other invertebrate taxa such as molluscs (Bouillon *et al.* 2002; Riera *et al.* 2002; Riera *et al.* 2004), and crustaceans (Bouillon *et al.* 2002; Rudnick and Resh 2005).

Mytilus edulis is found throughout the Scottish west coast inhabiting a large portion of the intertidal on shores of varying degrees of wave exposure (see Chapter 5). No research has been conducted examining the terrestrial influences on the stable isotope contribution of this marine species. Terrestrial input to the marine environment would range in size from a point source, such as a river outflow, to a more diffuse source which may be found at the head of large loch systems with low rates of water turnover.

6.1.6 Aims

The overall aim of this study was to determine the degree of variation in the stable isotope ratios of *M. edulis* within sampling sites on the scale of 10s to 100s of metres. From sampling mussels around the Scottish west coast (see Chapter 5), it was noted that mussels were found throughout the geographic area on both exposed and sheltered shores. It was hypothesized that sheltered shores found at the head of a loch will have a higher freshwater and terrestrial influence than exposed shores found outside loch systems which will have more of a pelagic, marine influence. As it was not feasible to sample on such a large spatial scale as that of Chapter 5, a secondary question was derived: do mussels directly exposed to a terrestrial influence have a differing stable isotopic signature from those further removed from a terrestrial influence? Understanding local influences, such as runoff, would aid in the interpretation of large-scale patterns.

Two null hypotheses were posed:

1. H_0 = No variation in mussel stable isotope ratios will be found within shores.
2. H_0 = No difference will be found in stable isotope ratios of mussels with a terrestrial compared to a marine influence.

To facilitate the comparison of the proximity to a terrestrial influence source, two river outputs in two loch systems were analysed. Mussels sampled at the river mouth would be expected to have an increased terrestrial influence due to the catchment of the river basin compared to mussels sampled away from the river mouth which would be expected to have a decreased terrestrial influence and a predicted increase from the marine environment.

6.2 Materials and Methods

To test the hypothesis of variation in mussel isotope signatures between shores with differing terrestrial and marine inputs, ten mussels (*M. edulis*) were collected at two sites, one in the Clyde system and one on the west coast of Scotland in February 2005 (Figure 6.1). At each site, mussels were sampled at the mouth of a stream and 100 metres from the stream mouth. Sites were located in Loch Creran (N56°31'54", W05°18'37") on the west coast and Loch Fyne (N55°54'06", W05°25'11") in the Clyde. Although the criterion for site location was primarily freshwater input, all locations were in relative shelter from wave exposure. The samples were taken back to the laboratory and frozen for later analysis.

6.2.1 Preparation procedures

After thawing, mussels were carefully prised open and the foot was dissected out. Previous work which looked at isotope signatures within the foot of *M. edulis* did not carry out lipid extraction (see Wiedemeyer and Schwamborn 1996) but it was felt that it would be beneficial to do so in order to determine whether the foot of the mussel concentrates lipids. The foot of each mussel was dissected in half longitudinally with each half placed in separate labelled bags so as to compare lipid extracted and non-lipid extracted samples from the same animal. Samples which did not have any lipid extracted were put in a 38 × 10 mm glass specimen vial and placed in a 60°C oven to dry to a constant weight.

6.2.1.1 Lipid extraction

Samples for lipid extraction were put in a marked test tube with 2 ml of chloroform methanol ensuring all the tissue was submerged in the liquid. The contents were decanted into a homogenising test tube and ground. The homogenised sample was decanted back into the original test tube with a further 3 ml of chloroform methanol ensuring the entire sample was covered in liquid. This was carried out for all samples with the homogenising equipment washed thoroughly between samples with 'decon 90' rinsed with acetone to ensure no cross-contamination. Caps were placed on all test tubes and left overnight in a fridge at 4°C. The next day, each sample was filtered through glass fibre filter paper and the remaining material put in a 38 × 10 mm glass specimen vial and placed in a 60°C oven to dry to a constant weight.

Once samples (both lipid extracted and non-lipid extracted) reached constant weight, they were removed from the oven, ground using an agate pestle and mortar, and weighed to 0.7 mg (±0.02 mg) in 5 × 3.5 mm tin capsules using a Perkin-Elmer AD-2Z Autobalance.

Isotope analysis was carried out at the Life Sciences Mass Spectrometry Facility at East Kilbride, Scotland. Samples were measured by continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Costech (model ECS 4010) elemental analyser (EA) combined with a ThermoFinnigan Delta Plus XP mass spectrometer. The stable isotope ratio was reported, in parts per thousand (‰) as

$$\delta X = [(R_{sample}/R_{standard})-1] \times 10^3 \qquad (6.1)$$

where X is the element ^{13}C or ^{15}N and R is the abundance ratio of heavy to light isotopes ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of that element. The standards used for carbon and nitrogen were V-Pee dee belemnite and atmospheric N_2 (air), respectively.

6.2.2 Data analysis

Data were analysed with a two-way ANOVA using the factors, and their interaction, of Loch and proximity to the stream mouth. After the test was carried out, the power of the performed test was analysed to determine the accuracy of the sample data in determining the variation of results within the factors and their interaction. As power refers to the probabilities of detecting a false null hypothesis, statistical discussions of the power of ANOVA testing depend upon the noncentral F distribution which is defined by ν_1, ν_2, and a third quantity known as the noncentrality parameter (Zar 1984).

To determine the power of the two-way ANOVA the methods of Zar (1984) were followed where a quantity (φ) related to the noncentrality parameter was calculated (formula 6.2) where k' is the number of levels of the factor being examined, MS is mean squares from the statistical output, and s^2 is the factor error of MS.

$$\varphi = \sqrt{\frac{(k'-1)(\text{factor MS}-s^2)}{k's^2}} \qquad (6.2)$$

The minimum detectable difference (δ) of a sample (n') can be calculated with formula 6.3 which can be rearranged (formula 6.4) to calculate φ.

$$\delta = \sqrt{\frac{2k's^2\varphi^2}{n'}} \qquad (6.3)$$

$$\varphi = \sqrt{\frac{n'\delta^2}{2k's^2}} \qquad (6.4)$$

Once φ has been calculated, it was possible to extrapolate a value for the power using the figure in Appendix 6.1. The value for v_2 was taken as 34 [v_2=k'(n-1)] and α as 0.05.

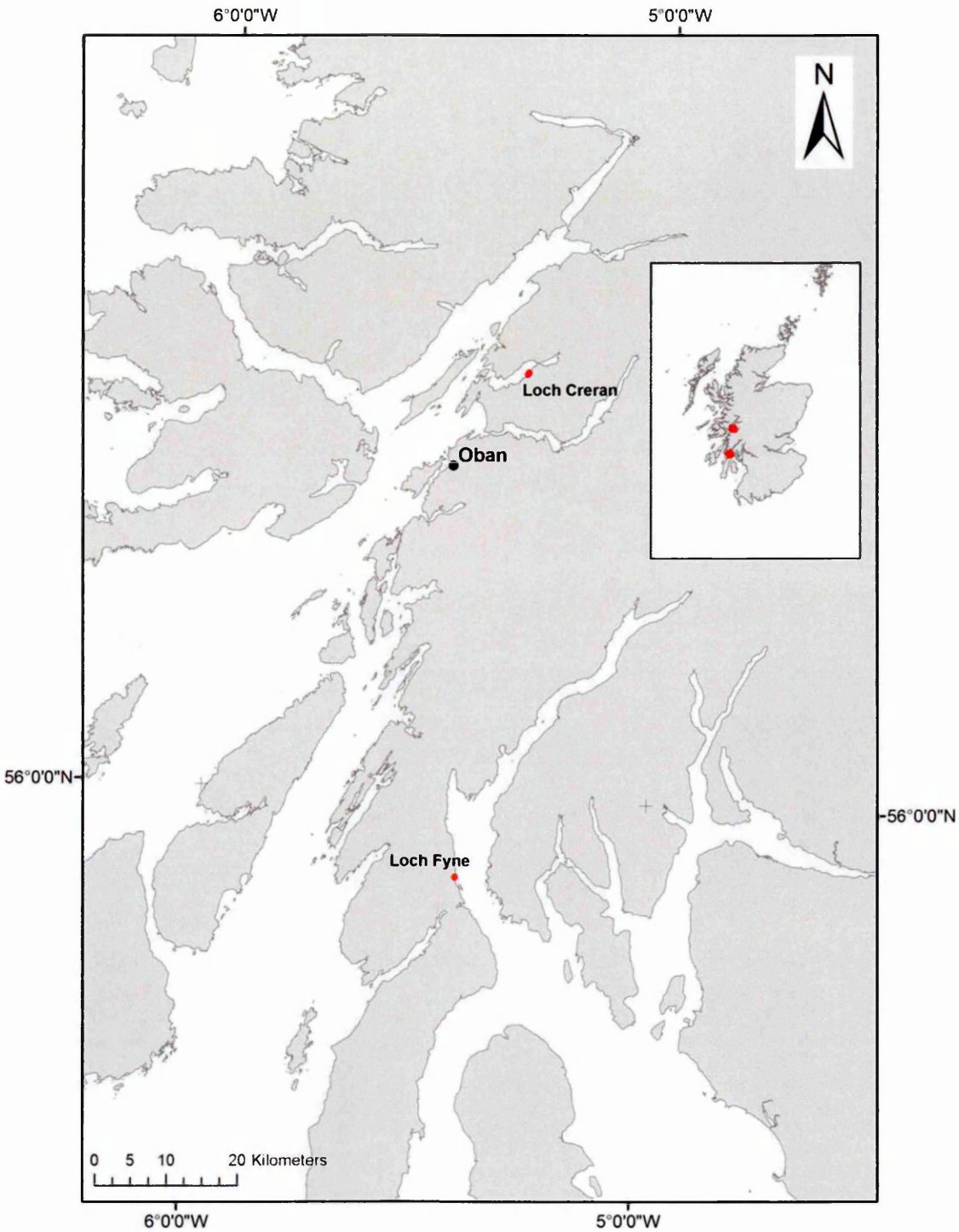


Figure 6.1 Locations of sites within Lochs Creran and Fyne to look at variation in mussel stable isotopes. Oban is marked on the map with a map insert depicting the location of the sites within Scotland.

6.3 Results

6.3.1 Variation within a site

The largest variation in $\delta^{13}C$ values was found at the site away from the stream mouth (a difference between the maximum and minimum of 1.09‰) in Loch Fyne while the site beside the stream mouth in Loch Fyne had the smallest variation in $\delta^{13}C$ with a range of 0.48‰ (Figure 6.2). The same pattern was found for $\delta^{15}N$ where the site away from the stream in Loch Fyne had the greatest variation with a range of 1.16‰ and the site beside the stream mouth had the least variation with a range of 0.92‰ (Figure 6.3).

6.3.2 Variation in loch and stream proximity

No significant difference was found in mussel $\delta^{13}C$ values between lochs but a significant difference was found between mussels beside the stream mouth and those away from the stream mouth, with those beside the stream mouth in Loch Creran having larger values (Table 6.1, Figure 6.2 and Figure 6.4). A highly significant difference was found with the $\delta^{13}C$ interaction of loch and stream proximity (Table 6.1).

Mussels in Loch Creran had significantly higher $\delta^{15}N$ values compared to those from Loch Fyne with sites beside the stream mouth also showing a significantly higher $\delta^{15}N$ value compared to those away from the stream mouth (Table 6.2, Figure 6.3 and Figure 6.4). No difference was found in the interaction between loch and stream proximity for $\delta^{15}N$ (Table 6.2).

Table 6.1 Results of the two-way analysis of variance of $\delta^{13}C$ values from the non-lipid extracted foot of *M. edulis*.

Factor	d.f.	SS	MS	F ratio	P value
Loch	1	0.088	0.088	1.21	0.279
Stream proximity	1	0.500	0.500	6.85	0.013
Interaction	1	2.259	2.259	30.97	<0.001
Residual	34	2.478	0.073		

Table 6.2 Results of the two-way analysis of variance of $\delta^{15}N$ values from the non-lipid extracted foot of *M. edulis*.

Factor	d.f.	SS	MS	F ratio	P value
Loch	1	2.490	2.490	20.50	<0.001
Stream proximity	1	0.562	0.562	4.63	0.039
Interaction	1	<0.001	<0.001	<0.01	1.000
Residual	34	4.130	0.122		

6.3.3 Power of two-way ANOVA

The power of the two-way ANOVA, measured as the likelihood of making a correct rejection of the null hypothesis, used to detect differences in stable isotope values between lochs, stream proximities, and their interaction was calculated for varying sample numbers using formulas 6.2; 6.3; and 6.4 (Figure 6.5). Differences between lochs of $\delta^{15}N$ and the interaction between lochs and stream proximity of $\delta^{13}C$ showed a similar trend with 10 samples being adequate to produce a power greater than 80%. To study the $\delta^{13}C$ interaction alone, only five samples would be needed (power = 78%).

No interaction term for $\delta^{15}N$ was calculated as the values for MS were too low (MS=0.00000004) leading to formula 6.2 square rooting a negative number. Differences between lochs in $\delta^{13}C$ would be undetectable unless there was a substantial increase in the sample number (n = 800 would produce a power of about 80%). Differences in stream proximity of both carbon and nitrogen showed an almost linear relationship and so an increase in sample number would increase the power of the test (for a power of 78%, sample numbers for $\delta^{13}C$ and $\delta^{15}N$ would have to be 25 and 45, respectively).

6.3.4 Lipid extraction

Although lipid extraction was carried out on all of the mussels sampled, it was not possible to analyse these samples. Of the samples which contained enough dry foot tissue for analyses (0.7 mg of tissue was required), it was not possible to grind them. The tissue was too thin to be ground with a pestle and mortar which was probably due to homogenisation of the tissue sample. Homogenisation caused the tissue sample to be thinned out and when combined with the chloroform methanol and dried, the sample was too thin to be ground.

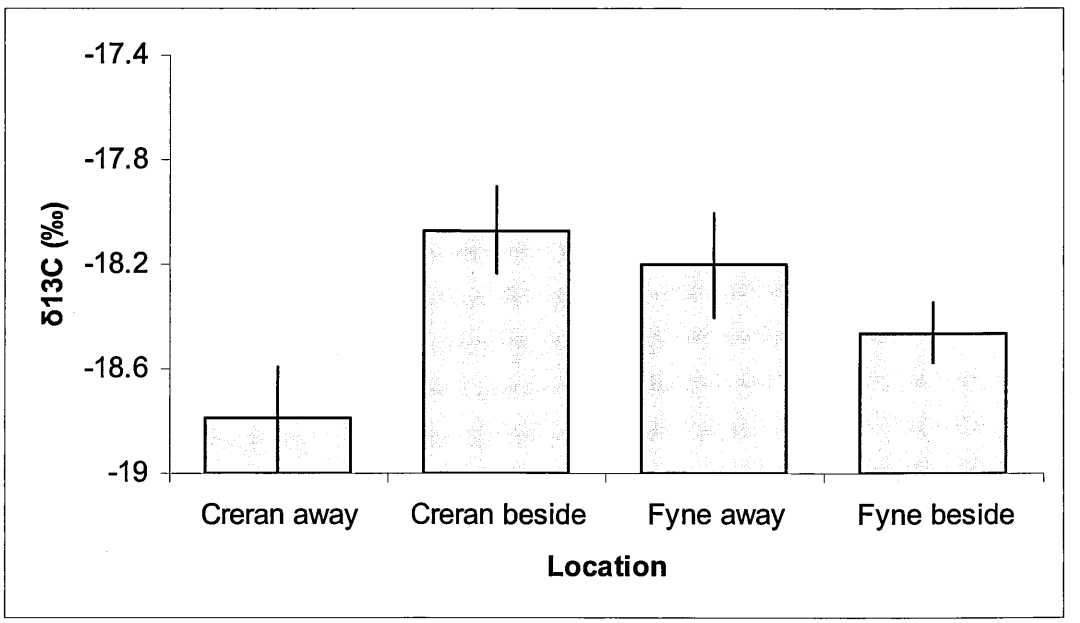


Figure 6.2 Mean $\delta^{13}C$ from samples collected away from a stream and beside a stream mouth in two lochs, Loch Creran on the west coast and Loch Fyne in the Clyde. 95% confidence intervals are shown.

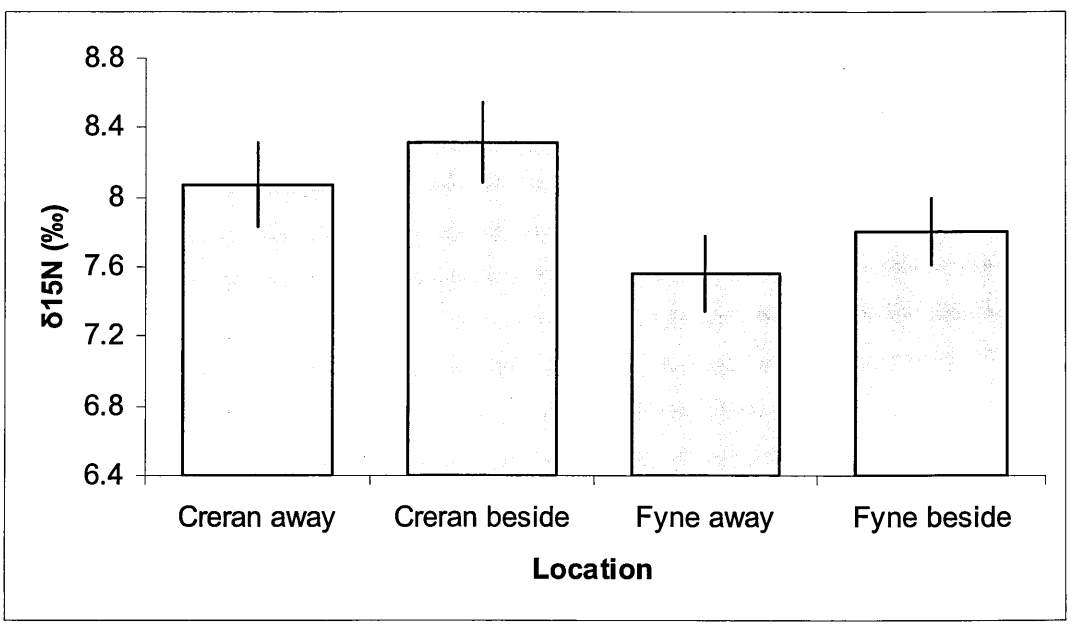


Figure 6.3 Mean $\delta^{15}N$ from samples collected away from a stream and beside a stream mouth in two lochs, Loch Creran on the west coast and Loch Fyne in the Clyde. 95% confidence intervals are shown.

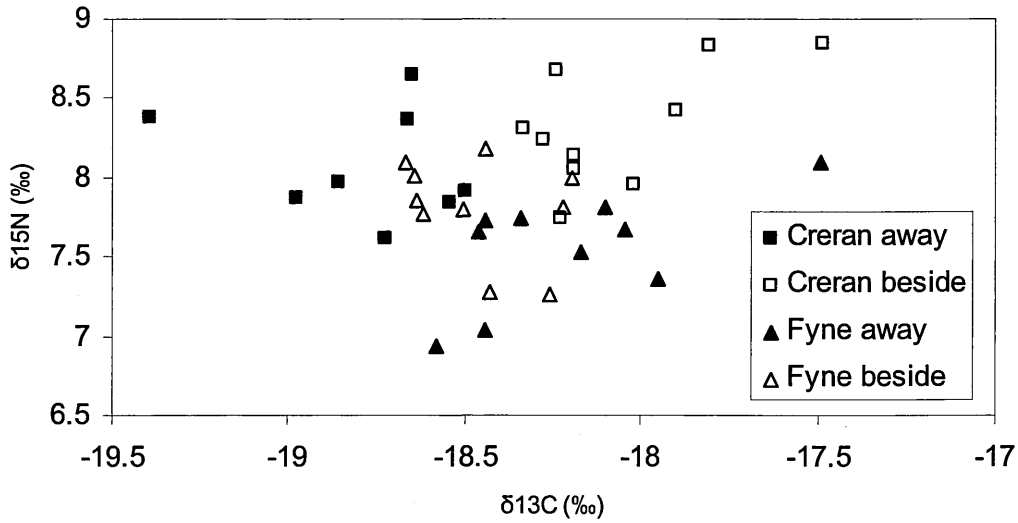


Figure 6.4 Stable isotope ratios for $\delta^{15}N$ and $\delta^{13}C$ from samples collected away from a stream (closed symbols) and beside a stream mouth (open symbols) in the two sites, Loch Creran on the west coast (squares) and Loch Fyne in the Clyde (triangles).

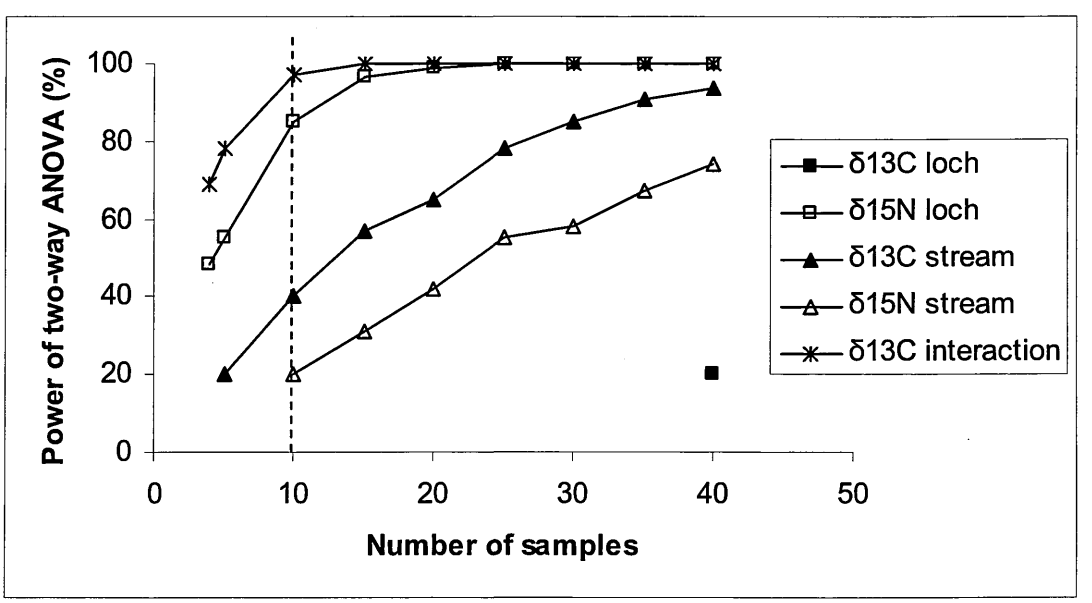


Figure 6.5 Power of the two-way ANOVA with varying sample numbers. Two factors, loch (squares) and stream proximity (triangles), with their interaction (*) are shown for both $\delta^{13}C$ (closed symbols) and $\delta^{15}N$ (open symbols). The dashed vertical line shows the sample size used.

6.4 Discussion

Previous estimation of stable isotope ratios of *M. edulis* have been limited to only three studies (Wiedemeyer and Schwamborn 1996; Kwak and Zedler 1997; Riera *et al.* 2002) with only nineteen, one, and five animals sampled, respectively. Mean $\delta^{13}C$ values from these studies ranged from -19.5 to -16.6‰ with the results of Kwak and Zedler (1997) found to be similar (the authors found a mean $\delta^{13}C$ value for *M. edulis* of -18.0‰) to those from this study. The values obtained from this study for $\delta^{15}N$ were found to be lower than those from previous studies of *M. edulis*. Kwak and Zedler (1997) recorded a mean $\delta^{15}N$ of 10‰ while Riera *et al.* (2002) recorded mean values ranging from 10.6‰ in summer to 12‰ in spring, although the latter value was obtained from one individual animal. Factors potentially contributing to the differences in the isotopic values observed in *M. edulis* in this study are exposure, mussel size, land-use of the surrounding area, freshwater input, and primary production.

Both sampling sites were in sheltered environments with mussels taken of a similar size range, although Fry and Allen (2003) showed no significant difference between nitrogen isotopic compositions of large (20-25 mm) and smaller (10-15 mm) zebra mussels. Studies have shown (McClelland and Valiela 1998; McKinney *et al.* 2001; Fry and Allen 2003) effects of terrestrial land use on stable isotopic signatures with nitrate often found to be the dominant N-nutrient flushed downstream from developing watersheds (Fry and Allen 2003). Nitrogen stable isotope values of this nitrate often increase with watershed development (McClelland and Valiela 1998). This would not be a problem at the sites in this study since development of the watershed was minimal as both watersheds were dominated by forestry areas (personal observation) with little human and agricultural input to the river systems. The maximum mean surface water nitrate

values along the west coast were not found to exceed 6μmol l^{-1} during winter and spring with little nitrate found during summer and autumn (Gillbrand *et al.* 2003).

6.4.1 Power of two-way ANOVA

In order to determine an efficient number of samples which will yield an accurate statistical outcome when examining mussel stable isotopes, it may be necessary to consider $\delta^{13}C$ and $\delta^{15}N$ separately. This is especially the case when examining mussels over large spatial scales. Zar (1984) noted that when the power is so very low that the experiment, as planned, ought not to be performed, the proposed experiment may be revised, perhaps by increasing the sample number, so as to render the results more likely to be conclusive. As mentioned previously, the number of samples needed to obtain a power of 80%, in detecting differences in $\delta^{13}C$ between lochs, would have to be increased to 800 individuals. This 2 000% increase would be hard to justify both financially and in time spent gathering and analysing samples. By revising the experimental setup and incorporating in an interaction, the estimated number of samples required would be dramatically reduced. However, this would lead to an increase in the chance of committing a Type I error at the smaller scale of stream proximity. As the complexity of the experiment increases it is clear that large numbers of samples would not be needed in order to obtain a statistically viable result, although too few samples would increase the chance of committing a Type II error. From these results, a sample size of between 20 and 45 would be adequate to ensure a reduction in Type II errors.

6.4.2 Lipid extraction

As biological tissues frequently vary in their lipid content, lipid enriched tissues (e.g. liver and muscle) are generally more depleted in ^{13}C than tissues that contain little fat (Pinnegar and Polunin 1999; Sotiropoulos *et al.* 2004). Previous studies used the soft tissue of the whole mussel (Bustamante and Branch 1996b; Post 2002; Riera *et al.* 2002; Rogers 2003; Garton *et al.* 2005; Howard *et al.* 2005) which is lipid rich and therefore requires lipid extraction. Only two known studies (Wiedemeyer and Schwamborn 1996; McKinney *et al.* 2002) examined the mussel foot with neither study carrying out lipid extraction and only Weidemeyer and Schmanborn (1996) examined the foot of *M. edulis*. It was felt that the mussel foot would be lipid poor and therefore not require lipid extraction and, according to Sotiropoulos *et al.* (2004), if analyses can be restricted to a specific tissue type, lipid extraction should not normally be necessary, particularly if samples are restricted to a single species or age class. Sotiropoulos *et al.* (2004) found that the removal of lipids increased $\delta^{13}C$ by 3.4‰ in whole fish which could have consequences for interpreting the results. Such an increase could lead to an underestimate of the contribution of one source of production (e.g. macrophytes) and overestimate the contribution of another (e.g. phytoplankton) in an aquatic environment (Sotiropoulos *et al.* 2004) as well as possibly incorrectly altering the species trophic level as Post (2002) noted a 3.4‰ difference in $\delta^{13}C$ between trophic levels.

6.4.3 Summary

This study has given some insight into the complexity of stable isotope signatures of *M. edulis* in Scotland. Although both null hypotheses were rejected, many questions still remain unanswered. Clear and significant differences were found in $\delta^{15}N$ between areas of high (Loch Fyne in the Clyde) and low (Loch Creran on the west coast) pelagic primary productivity although only one loch was analysed in each area. Results from Loch Fyne may be indicative of what is found within the water column of the system whereas those from Loch Creran may be driven more from terrestrial inputs of the stream. It should be noted, however, that Loch Fyne has a substantially larger surface area to that of Loch Creran which has a limited exchange due to a smaller mouth opening compared with Loch Fyne (Figure 6.1). Comparing sites of differing exposure within the two regions under study will give a good indication of differences in $\delta^{13}C$ and $\delta^{15}N$ between pelagic marine dominated environments (exposed areas) and marine environments with potential for more terrestrial influences (sheltered areas). As well as spatial (both large and small scale) effects, another obvious question which should be posed is: Is there a temporal effect of stable isotope signatures on *M. edulis* in western Scotland? The complexity of the results of this study may be due to the time of year that sampling took place and as Fry and Allen (2003) noted, the maximum $\delta^{15}N$ values occurred at the end of the strong summer phytoplankton bloom, consistent with phytoplankton foods having high $\delta^{15}N$ values.

Chapter 7 General discussion

The initial aim of this investigation was to test for differences in community structure between two regions of contrasting pelagic primary productivity. It was hypothesised that the variation in community structure between these regions, a macroalgae dominated west coast and a filter feeder dominated Clyde, was due to the influence of an increased bottom-up influence in the Clyde compared to that of the west coast. To some extent this initial hypothesis was supported with regard to the abundance of macroalgae and barnacle species, although at a smaller scale, site-specific variation was found to be of greater importance (Chapter 2). The occurrence of *Patella vulgata* (L., 1758) and *Littorina littorea* (L., 1758), and the cover of macroalgae and barnacles were found to be significantly greater at inner loch sites with *Nucella lapillus* (L., 1758) and *Mytilus edulis* (L., 1758) found to dominate mouth sites. Variation between sites was most probably due to the effects of wave exposure increasing water flow at sites at the mouth of loch systems. Although sites were chosen to maximise similarities, such as wave exposure, it is conceivable that sites situated at the mouth of lochs will be prone to an increased wave exposure due to an increased fetch compared with inner sites which would have increased protection from the proximity of the opposite facing shoreline reducing the fetch at inner sites. By extrapolating wave exposure values of inner and mouth sites from the findings of Chapter 5, it was clear that inner sites (range 2.8 to 2.9 $km.kt^2\ s^{-2}$) were slightly more sheltered than sites at the mouth of the loch (range 2.9 to 3.2 $km.kt^2\ s^{-2}$). High flow sites, characterised by high densities of herbivorous and carnivorous gastropods and their predators, have been shown to have an increased growth rate for both barnacles and *N. lapillus* while *M. edulis* had a marginally lower growth rate and *L. littorea* showed no difference in growth compared to that of low flow sites (Leonard *et al.* 1998). These results corroborated the findings of the present study which showed that the growth rates of *M. edulis* (section 3.3.4) were found to be significantly slower at mouth sites. Barnacles, however, did not follow this pattern with

changes in length of *Semibalanus balanoides* (L., 1767) found to be increased at the mouth of Lochs Long and Melfort and at the inner positions of Lochs Fyne and Caolisport (section 2.3.4). Length changes in *Chthamalus montagui* Southward, 1976 from the 2003 and pre 2003 settlements did follow the findings of Leonard *et al.* (1998) with greater length increases recorded at the mouth of lochs (section 2.3.6).

7.1 Association of macroalgae between regions and with the mussel, *M. edulis*

A diagrammatic view of the interactions, and potential interactions, which were observed in the communities of the two regions under study, is shown in Figure 7.1. From this representation it is clear that more information is needed on the influence which macroalgae may have on the community. In the grazing and predation experiments (Chapter 4), sporelings of *Fucus vesiculosus* L., 1753 were only recorded within cages at Loch Caolisport one month from the start of the experiment and no macroalgal species were recorded within cages at the remaining three lochs. Barnacle cover was also found to be affected by the absence of *L. littorea* which was probably due to an indirect effect of increased algal cover as a result of reduced grazing pressure. Macroalgae have been shown to have negative impacts on barnacle settlement (Jenkins *et al.* 1999c; Benedetti-Cecchi *et al.* 2000) and large mussel settlements (Erlandsson and McQuaid 2004) although the latter authors noted a positive effect of macroalgae on small mussel settlements. As mentioned previously, the association between mussels and macroalgae is well known (Hunt and Scheibling 1995) with extensive macroalgal cover able to directly affect mussel cover through limiting settlement (Figure 7.1a) and large mussel cover able to affect macroalgal cover (Figure 7.1b). The latter was described by Menge (1978) who noted that in the absence of *Nucella*, *Mytilus* pulls *Fucus* into the matrix of the mussel bed, eventually either smothering it or tearing it

loose when the mussels are washed off the shore during storms. Over a prolonged time period of predator absence, areas initially covered with *Fucus* would become mussel dominated, hence the fucoid canopy is dependent on the removal of *Mytilus* by *Nucella* (Menge 1978). The abundance of *N. lapillus* was not found to be significantly different between regions and therefore would not have a significant negative effect on *M. edulis* abundance. With an abundance of mussels recorded at both sites of Loch Long and few macroalgae species present, the establishment of a macroalgal dominated shore from a mussel dominated would potentially depend on a large disturbance event or a significant increase in predation limiting the mussel cover.

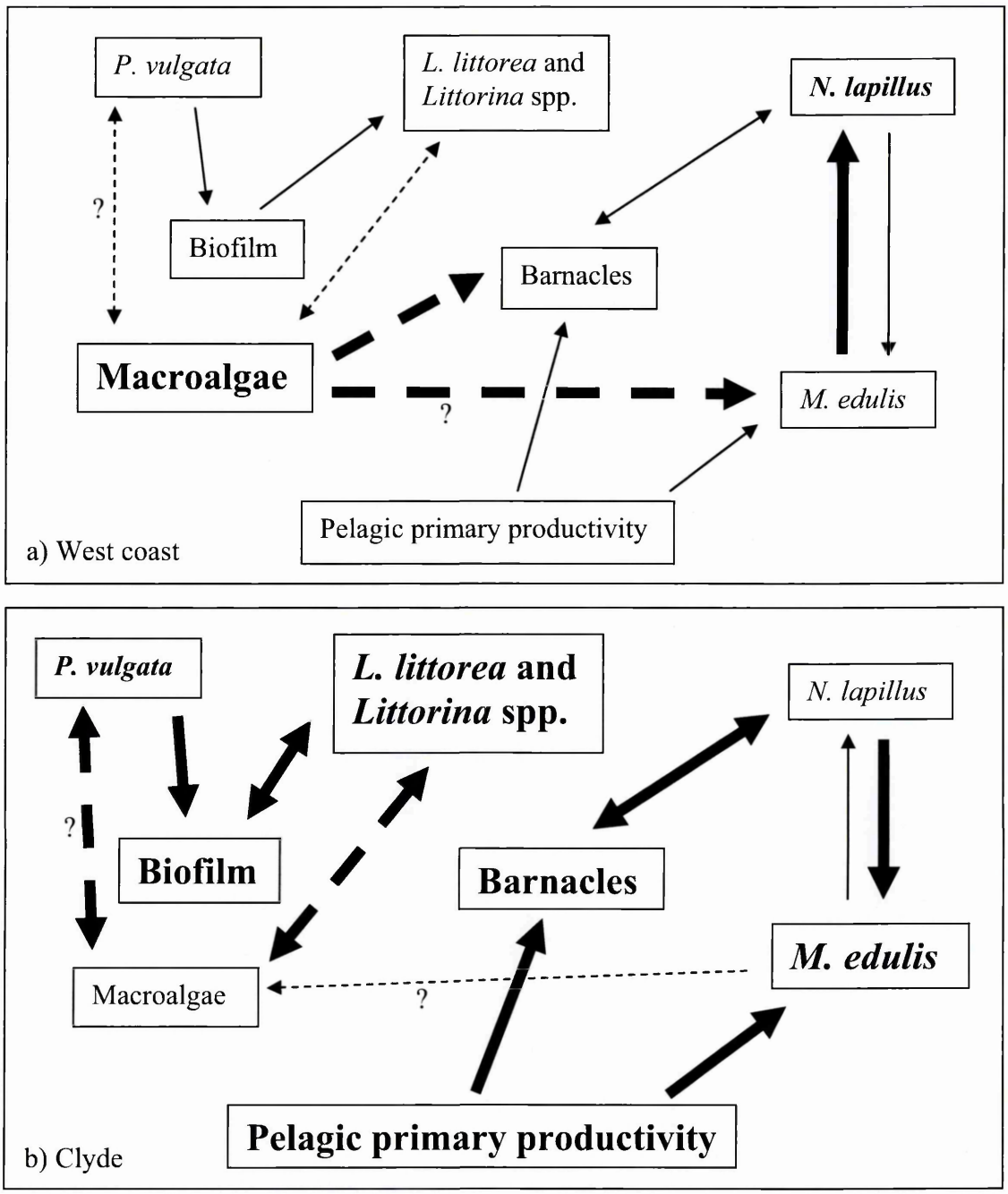


Figure 7.1 A diagrammatic representation of the findings from (a) the west coast and (b) the Clyde. Bold lettering indicates prevalence within the particular area with larger lettering representing a significant difference in abundance between the two regions. Line thickness indicates strength of link between groups and arrowheads represent the direction of the link. Broken lines are estimated links with "?" indicating no available data.

7.2 The role of the mussel, *M. edulis*, as an indicator of wave exposure and terrestrial influences

Changes in mussel abundance (Chapter 2), growth rates (Chapter 3), predation rates by *N. lapillus* (Chapter 4), the effects of wave exposure on size and biomass (Chapter 5), and stable isotope analysis in relation to freshwater influences (Chapter 6) were all examined. Mussels were abundant at both sites in Loch Long with few individuals recorded at Lochs Fyne, Caolisport, and Melfort. However, this species was found throughout the wave exposure gradient around western Scotland (Chapter 5). Wave exposed sites were found to be dominated by small mussels (length and biomass) with increased predation rates recorded for this size category (section 4.3.3). Loch Caolisport was the only site where large mussels were preyed on, which may have been due to a change in diet of *N. lapillus* from barnacles to mussels. An alternate explanation would be that *Nucella* have 'learnt' to avoid large mussels in order to minimise the chances of becoming caught in the byssi of the mussel and potentially becoming smothered and die. The latter was represented by a strong downward link from *Nucella* to *Mytilus* in the Clyde (Figure 7.1b) while a strong upward link on the west coast corresponded with increased predation (Figure 7.1a). Stable isotope analysis demonstrated a clear difference between Lochs Fyne and Creran which may have been due to food quality and terrestrial inputs, respectively. Small scale between site variability was found to be much greater than between region variability and therefore, despite potential differences in food availability among regions, factors varying on small scales, including those associated with wave exposure, may be more important in structuring mussel populations.

7.3 The role of bottom-up processes on the western shoreline of Scotland

Previous studies exploring population and community dynamics focused on top-down effects (i.e. communities structured through predation pressures) and it is only recently that ecologists have started to recognise that top-down and bottom-up (i.e. productivity variation) processes act in concert to influence the dynamics of the community (Hunter and Price 1992; Menge 1992; Menge *et al.* 2003). Due to this dynamic linkage, a stronger predation pressure would be expected to occur at sites where productivity is prevalent as a result of an upward cascade within the food web (Hunter and Price 1992; Nielsen and Navarrete 2004). An increase in barnacle and mussel cover were noted in the Clyde (Figure 7.1b) but only one predator, *N. lapillus*, was examined with no significant difference found in abundance between the two regions (Chapter 2) and no difference in rates of predation on barnacles were recorded (Chapter 4) for this species. Trophically higher predators, such as starfish, crabs, and fish, were not studied but would be expected to play a significant role during high tide. Whether the abundance and/or voracity of these other predators were greater in the Clyde may require further study.

Nielson (2003) noted that a major problem with studying intertidal communities in relation to bottom-up processes is that they develop more slowly relative to top-down effects. In order to test whether a system is driven from the bottom up experiments would have to be conducted over much longer time periods (several years). The initial phase, Chapter 2, of this study ran for two years but not all experiments were conducted over the same time period which poses additional questions (see section 7.4) as to the significance of top-down control within these two systems. On a large scale, between regions, bottom-up influences most probably exerted the greatest influence on the

structuring of the community. Even at smaller scales of site-specific variation, the influence of bottom-up processes is evident with increased emphasis on smaller-scale processes such as water flow rates which have a direct affect on rates of food supply.

7.4 Future work and improvements to the current experimental design

This study has shown that large scale oceanographic conditions influencing pelagic primary productivity have the potential to structure intertidal communities but such large scale studies should be run in conjunction with experiments focusing on smaller scale, site-specific effects. For this reason, the predation and grazing experiments (Chapter 4) should have been carried out at both inner and mouth sites with the experiment run in parallel to that of Chapter 2. Increasing the length of the grazing experiments, in conjunction with an initial increased frequency of sampling, would determine whether rates of algal succession varied between lochs, as implied by the results (section 4.3.2), and contribute to the understanding of why the west coast is dominated by macroalgae and the Clyde by filter feeders. Predation rates of *N. lapillus* on *M. edulis* should be investigated further, examining prey preference in relation to predator loch of origin. The results from this study suggest that *Nucella* at Loch Long may have learnt to avoid large mussels thus reducing their chances of becoming ensnared by the mussel byssi. This hypothesis could be easily tested by increasing the duration of the study from one month to at least one year which would also examine any temporal changes in predation rates.

The main area of concern when examining growth rates of *N. lapillus*, *L. littorea*, and *P. vulgata* was the lack of information from rapidly growing juvenile and small animals (Chapter 3). Increasing the number of marked *Nucella* and *Littorina* to at least 100

individuals per species, a minimum of half should be classed as juvenile or of a small size, would increase the number of animals recaptured over time assuming a 10% recapture rate as seen in the present study. Photographic analysis of limpet growth was found to be highly effective for larger animals with established home scars but smaller individuals were not consistently found in the same location over time. This may be due to increased mortality of smaller limpets or, due to the reduced surface area required to secure their shells to the substratum, the ability to utilise different areas of free space without being constrained by a home scar. Reproduction is a major factor contributing to changes in growth rates and should be studied, not only in the four species analysed in Chapter 3, but also for *S. balanoides*, *C. montagui*, and *Chthamalus stellatus* (Poli, 1791) in Chapter 2.

Clear results were obtained for *M. edulis* size and biomass in relation to variation in wave exposure (Chapter 5) but it was unclear as to what factor, or factors, such as growth rates (Chapter 3), predation intensity (Chapter 4), freshwater influence (Chapter 6), or quality of food were responsible for these findings. Food quality is known to be more important than the quantity of food (Page and Ricard 1990; Penney *et al.* 2001) and although data were available regarding the quantity of the food (Figure 1.1), no data were collected in order to determine its quality. The increased spatial scale of the study examining varying wave exposure on *M. edulis* (Chapter 5) was designed with the intention of minimising time spent at each site while maximising the number of sites visited per day. For this reason it would not have been practical to conduct in-depth examinations into recruitment rates, predation pressures and variation into growth rates. Further examination into the positive feedback mechanism of mussels in semi-enclosed embayments (see Archambault *et al.* 1999 and section 5.4) should be investigated further in relation to differing pelagic primary productivity, surface area of the loch, and

the size of the loch opening in order to determine variation in mussel growth and recruitment.

The pilot study of mussel stable isotope analysis (Chapter 6) should be extended over a larger spatial scale. The obvious next step would be to increase the number of sites in both the Clyde and west coast in conjunction with sites within lochs in order to test for regional and site-specific differences. This sample collection would have to be run for a minimum of one year in order to test for temporal changes in the stable isotope signatures. It would then be feasible to increase the experiment over a larger spatial scale examining differences between wave exposures testing the hypothesis that stable isotope signatures at wave exposed sites will be influenced by a pelagic marine source and those at wave sheltered sites by terrestrial influences.

The overall aim of the study was to test whether differences in the structure and functioning of intertidal communities exist between two areas of contrasting primary productivity. The results of this study failed to disprove the overall null hypothesis (Chapter 1) with little evidence to suggest that pelagic primary production in the Clyde and the west coast was the major driving force within these systems at small spatial scales. However, the results did emphasise the importance of more local, smaller-scale processes such as water flow, with the position within a loch found to be highly significant (Chapter 2). Influences of large-scale effects on intertidal communities, such as oceanographic processes (e.g. regions of upwelling versus regions of downwelling) and climate change, are of increasing importance and interest which should be studied concurrently with smaller-scale, site specific effects in mind.

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Appendix 2

Appendix 2.1 Sites visited to estimate abundance of flora and fauna on the west coast and the Clyde system of Scotland.

Region	Loch	Position within loch	Abbreviation	Latitude	Longitude
Clyde	Fyne	mouth *	F mou	55.8785	-5.3186
Clyde	Fyne	inner *	F inn	56.0771	-5.2532
Clyde	Fyne	upper	F upp	56.1417	-5.1434
Clyde	Long	mouth * †	L mou	56.0030	-4.8535
Clyde	Long	inner * †	L inn	56.0389	-4.8679
Clyde	Long	upper	L upp	56.1232	-4.8217
West coast	Caolisport	mouth * †	C mou	55.8681	-5.6458
West coast	Caolisport	inner * †	C inn	55.9150	-5.6034
West coast	Caolisport	upper †	C upp	55.9307	-5.6008
West coast	Etive	outer	E out	56.4553	-5.4363
West coast	Melfort	mouth *	M mou	56.2086	-5.5596
West coast	Melfort	inner2 *	M inn2	56.2434	-5.5379
West coast	Melfort	outer	M out	56.1434	-5.6029
West coast	Melfort	inner1	M inn1	56.2421	-5.5396

* indicates sites used on the three monthly survey of fixed sites.

† indicates sites used in mussel transplant experiment of Chapter 3.

Appendix 2.2 SACFOR scaling system used to estimate abundance of intertidal flora and fauna.

ABBREVIATIONS
E = Extremely Abundant
S = Super Abundant
A = Abundant
C = Common
F = Frequent
O = Occasional
R = Rare
NS = Not seen but looked for

Algae
E >90% cover
S 60-90%
A >30%
C 5-30%
F <5% cover, zone still apparent
O Scattered individuals, zone indistinct
R Few plants found in 30min. search

Lichens, *Lithothamnia*
E >80% cover
S 50-79%
A >20% cover at some levels
C 1-20% cover, zone well defined
F Large scattered patches, zone ill defined
O Widely scattered, small patches
R Few small patches found in 30min. search

Topshells, anemones, sea urchins
E >10/10cm^2
S 5-9/10cm^2
A 1-4/10cm^2
C 5-9 m^{-2}
F 1-4 m^{-2}
O <1 m^{-2}
R always <1 m^{-2}

Large periwinkles, *Littorina* spp., limpets, dogwhelks
E >200 m^{-2}
S 100-200 m^{-2}
A >50 m^{-2}
C 10-50 m^{-2}
F 1-10 m^{-2}
O <1 m^{-2}
R Only 1 or 2 found in 30min. search

Mussels
E >80% cover
S 50-79%
A >20%
C Large patches
F Many scattered individuals & small patches
O Scattered individuals, no patches
R Few found in 30 min. search

Barnacles
E >5 cm^{-2}
S 3-5 cm^{-2}
A >1 cm^{-2}, rocks well covered
C 0.1-1 cm^{-2}, up to ⅓ of rock space covered
F 100-1000 m^{-2}, individuals never >10 cm apart
O 1-100 m^{-2}, few within 10cm of each other
R Few found in 30 min. search

Appendix 2.3 Check list of flora and fauna species used for abundance estimates.

Lichens

Xanthoria parietina
Verrucaria maura
Lichina pygmaea

Algae

Enteromorpha spp.
Cladophora rupestris
Ulva lactuca

Pelvetia canaliculata
Fucus spiralis
F. vesiculosus
Ascophyllum nodosum
F. serratus
Halidrys siliquosa
Himanthalia elongate
Laminaria digitata
Chorda filum
Alaria esculenta

Laurencia spp.
Chondrus crispus
Polysiphonia lanosa (on *Ascophylum*)
Corallina officinalis
Corallina crusts – high pools
Corallina crusts – lower shore

Mollusca

Littorina neritoides
L. rudis
L. obtusata
L. littorea
Nucella lapillus
Patella vulgate
Gibbula umbilicalis
Mytilus edulis

Crustacea

Chthamalus montagui
C. stellatus
Semibalanus balanoides
Elminius modestus
Carcinus maenas

Other fauna

Actinia equina
Spirorbis spirorbis (*borealis*)
Pomatoceros triqueter

Appendix 2.4 Results of the summary statistics for barnacle cover using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
Region	1	37.702	37.702	1.98	0.288
Loch(Region)	2	43.330	21.665	0.65	0.569
Position	1	1.304	1.304	0.14	0.740
Height	1	22.945	22.945	1.47	0.344
Cleared	1	2.407	2.407	0.16	0.728
Region×Position	1	9.508	9.508	1.02	0.408
Region×Height	1	2.122	2.122	0.14	0.746
Region×Cleared	1	0.605	0.605	0.04	0.859
Position×Height	1	10.327	10.327	2.72	0.102
Position×Cleared	1	7.557	7.557	1.99	0.161
Height×Cleared	1	21.218	21.218	5.59	0.020
Position×Loch(Region)	2	20.500	10.250	2.70	0.072
Height×Loch(Region)	2	33.994	16.997	4.48	0.013
Cleared×Loch(Region)	2	30.618	15.309	4.03	0.020
Region×Position×Height	1	6.767	6.767	1.78	0.185
Region×Position×Cleared	1	2.478	2.478	0.65	0.421
Region×Height×Cleared	1	2.668	2.668	0.70	0.404
Position×Height×Cleared	1	0.760	0.760	0.20	0.655
Residual	113	428.949	3.796		
Total	135				

Appendix 2.5 Nested ANOVA of barnacle cover during August 2003 and March 2004 (* denominator of the F test is zero).

	d.f.	SS	MS	F ratio	P value
August 2003					
Region	1	6.886	6.886	0.93	0.410
Loch(Region)	2	19.505	9.753	0.40	0.709
Position	1	15.146	15.146	4.33	0.089
Height	1	1.494	1.494	0.08	0.796
Cleared	1	0.837	0.837	0.16	0.714
Region×Position	1	11.137	11.137	3.16	0.168
Region×Height	1	3.365	3.365	0.22	0.675
Region×Cleared	1	0.508	0.508	0.10	0.765
Position×Height	1	0.132	0.132	0.04	0.845
Position×Cleared	1	2.589	2.589	0.76	0.386
Height×Cleared	1	37.808	37.808	11.10	0.001
Position×Loch(Region)	2	7.123	3.562	1.05	0.356
Height×Loch(Region)	2	43.918	21.959	6.45	0.002
Cleared×Loch(Region)	2	12.852	6.426	1.89	0.158
Region×Position×Cleared	1	4.034	4.034	1.18	0.280
Region×Height×Cleared	1	9.053	9.053	2.66	0.107
Position×Height×Cleared	1	0.322	0.322	0.09	0.759
Residual	86	292.996	3.407		
Total	107				
March 2004					
Region	1	16.3	16.3	0.46	0.667
Loch(Region)	1	43.7	43.7	*	
Position	1	1163.3	1163.3	9.55	0.319
Height	1	3043.8	3043.8	*	
Cleared	1	12.6	12.6	0.02	0.891
Region×Position	1	332.4	332.4	2.73	0.450
Region×Height	1	16.5	16.5	*	
Region×Cleared	1	1018.8	1018.8	1.93	0.297
Position×Cleared	1	117.7	117.7	0.25	0.618
Height×Cleared	1	1776.5	1776.5	3.79	0.056
Position×Loch(Region)	1	146.8	146.8	0.31	0.578
Height×Loch(Region)	1	0.1	0.1	<0.01	0.987
Cleared×Loch(Region)	1	556.3	556.3	1.19	0.281
Region×Position×Cleared	1	543.8	543.8	1.16	0.286
Region×Height×Cleared	1	61.5	61.5	0.13	0.719
Residual	57	26711.4	468.6		
Total	72				

Appendix 2.6 Nested ANOVA of barnacle cover during September 2004 and March 2005.

	d.f.	SS	MS	F ratio	P value
September 2004					
Region	1	13450.1	13450.1	27.51	0.002
Loch(Region)	2	1214.1	607.0	0.55	0.651
Position	1	1218.0	1218.0	3.18	0.209
Height	1	38.5	38.5	0.10	0.752
Cleared	1	62.3	62.3	0.08	0.788
Region×Position	1	116.7	116.7	0.30	0.633
Region×Height	1	1604.1	1604.1	4.18	0.045
Region×Cleared	1	11.2	11.2	0.02	0.909
Position×Cleared	1	243.2	243.2	0.63	0.429
Height×Cleared	1	1124.8	1124.8	2.93	0.091
Position×Loch(Region)	2	765.9	382.9	1.00	0.374
Cleared×Loch(Region)	2	2170.0	1085.0	2.83	0.066
Region×Position×Cleared	1	1901.5	1901.5	4.96	0.029
Region×Height×Cleared	1	645.1	645.1	1.68	0.199
Residual	68	26086.4	383.6		
Total	85				
March 2005					
Region	1	5310.4	5310.4	1.58	0.315
Loch(Region)	2	15336.4	7668.2	1.17	0.405
Position	1	649.7	649.7	0.20	0.695
Height	1	3477.1	3477.1	2.15	0.235
Cleared	1	453.8	453.8	0.74	0.403
Region×Position	1	4835.6	4835.6	1.44	0.342
Region×Height	1	425.4	425.4	0.27	0.639
Region×Cleared	1	196.7	196.7	0.32	0.581
Position×Height	1	732.1	732.1	1.33	0.252
Position×Cleared	1	3418.0	3418.0	6.22	0.015
Height×Cleared	1	2749.0	2749.0	5.00	0.028
Position×Loch(Region)	2	9505.4	4752.7	8.64	<0.001
Height×Loch(Region)	2	6427.2	3213.6	5.84	0.004
Cleared×Loch(Region)	2	1514.1	757.1	1.38	0.259
Region×Position×Cleared	1	902.2	902.2	1.64	0.204
Region×Height×Cleared	1	2587.9	2587.9	4.71	0.033
Position×Height×Cleared	1	705.6	705.6	1.28	0.261
Residual	74	40686.4	549.8		
Total	95				

Appendix 2.7 Results of the summary statistics for macroalgae cover using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
Region	1	2759.0	2759.0	21.48	0.025
Loch(Region)	2	262.7	131.3	0.05	0.952
Position	1	271.3	271.3	0.14	0.746
Height	1	2.7	2.7	0.01	0.914
Cleared	1	21.4	21.4	0.06	0.826
Region×Position	1	119.6	119.6	0.06	0.828
Region×Height	1	134.3	134.3	0.72	0.475
Region×Cleared	1	126.7	126.7	0.37	0.604
Position×Height	1	5.8	5.8	0.05	0.820
Position×Cleared	1	265.9	265.9	2.38	0.126
Height×Cleared	1	189.5	189.5	1.70	0.195
Position×Loch(Region)	2	4597.6	2298.8	20.59	<0.001
Height×Loch(Region)	2	388.4	194.2	1.74	0.180
Cleared×Loch(Region)	2	701.8	350.9	3.14	0.047
Region×Position×Height	1	38.7	38.7	0.35	0.557
Region×Position×Cleared	1	198.1	198.1	1.77	0.186
Region×Height×Cleared	1	73.7	73.7	0.66	0.418
Position×Height×Cleared	1	10.3	10.3	0.09	0.762
Residual	113	12618.5	111.7		
Total	135				

Appendix 2.8 Nested ANOVA of macroalgae cover during August 2003 and March 2004 (* denominator of the F test is zero).

	d.f.	SS	MS	F ratio	P value
August 2003					
Region	1	1567.0	1567.0	3.59	0.145
Loch(Region)	2	1063.1	531.5	0.27	0.786
Position	1	435.1	435.1	0.33	0.614
Height	1	22.9	22.9	0.20	0.664
Cleared	1	9.8	9.8	0.02	0.887
Region×Position	1	906.3	906.3	0.56	0.528
Region×Height	1	33.3	33.3	0.23	0.635
Region×Cleared	1	51.0	51.0	0.13	0.737
Position×Height	1	20.0	20.0	0.07	0.787
Position×Cleared	1	232.5	232.5	0.85	0.358
Height×Cleared	1	1.9	1.9	0.01	0.934
Position×Loch(Region)	2	4004.2	2002.1	7.35	0.001
Height×Loch(Region)	2	131.0	65.5	0.24	0.787
Cleared×Loch(Region)	2	1013.3	506.7	1.86	0.162
Region×Position×Cleared	1	226.8	226.8	0.83	0.364
Region×Height×Cleared	1	3.9	3.9	0.01	0.905
Position×Height×Cleared	1	37.8	37.8	0.14	0.711
Residual	86	23430.6	272.4		
Total	107				
March 2004					
Region	1	1635.5	1635.5	42.23	0.065
Loch(Region)	1	35.2	35.2	0.01	0.943
Position	1	325.0	325.0	0.07	0.831
Height	1	35.4	35.4	0.48	0.654
Cleared	1	45.3	45.3	0.05	0.859
Region×Position	1	15.9	15.9	<0.01	0.962
Region×Height	1	392.6	392.6	5.37	0.347
Region×Cleared	1	1.1	1.1	<0.01	0.978
Position×Cleared	1	206.9	206.9	0.75	0.391
Height×Cleared	1	498.8	498.8	1.80	0.185
Position×Loch(Region)	1	4226.2	4226.2	15.25	<0.001
Height×Loch(Region)	1	84.5	84.5	0.30	0.583
Cleared×Loch(Region)	1	1323.7	1323.7	4.78	0.033
Region×Position×Cleared	1	130.0	130.0	0.47	0.496
Region×Height×Cleared	1	178.8	178.8	0.65	0.425
Residual	58	16078.4	277.2		
Total	73				

Appendix 2.9 Nested ANOVA of macroalgae cover during September 2004 and March 2005.

	d.f.	SS	MS	F ratio	P value
September 2004					
Region	1	2409.3	2409.3	8.35	0.034
Loch(Region)	2	772.4	386.2	0.10	0.910
Position	1	627.3	627.3	0.16	0.724
Height	1	80.6	80.6	0.40	0.529
Cleared	1	3839.7	3839.7	12.97	0.019
Region×Position	1	142.6	142.6	0.04	0.864
Region×Height	1	109.4	109.4	0.54	0.464
Region×Cleared	1	2047.2	2047.2	6.91	0.052
Position×Cleared	1	361.1	361.1	1.79	0.185
Height×Cleared	1	2249.9	2249.9	11.17	0.001
Position×Loch(Region)	2	7847.3	3923.6	19.48	<0.001
Cleared×Loch(Region)	2	772.3	386.2	1.92	0.155
Region×Position×Cleared	1	217.2	217.2	1.08	0.303
Region×Height×Cleared	1	2081.4	2081.4	10.34	0.002
Residual	68	13694.5	201.4		
Total	85				
March 2005					
Region	1	461.5	461.5	2.32	0.147
Loch(Region)	2	340.8	170.4	0.07	0.932
Position	1	773.1	773.1	0.41	0.584
Height	1	203.6	203.6	0.87	0.373
Cleared	1	530.3	530.3	1.93	0.195
Region×Position	1	663.2	663.2	0.34	0.615
Region×Height	1	5.5	5.5	0.02	0.881
Region×Cleared	1	245.0	245.0	0.89	0.371
Position×Height	1	4.3	4.3	0.02	0.888
Position×Cleared	1	310.7	310.7	1.43	0.236
Height×Cleared	1	323.5	323.5	1.49	0.226
Position×Loch(Region)	2	5625.7	2812.8	12.95	<0.001
Height×Loch(Region)	2	516.7	258.3	1.19	0.310
Cleared×Loch(Region)	2	822.2	411.1	1.89	0.158
Region×Position×Cleared	1	302.2	302.2	1.39	0.242
Region×Height×Cleared	1	652.0	652.0	3.00	0.087
Position×Height×Cleared	1	3.4	3.4	0.02	0.901
Residual	74	16078.6	217.3		
Total	95				

Appendix 2.10 Results of the summary statistics for *P. vulgata* abundance using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
Region	1	19.44	19.44	0.29	0.643
Loch(Region)	2	154.69	77.35	2.91	0.221
Position	1	111.30	111.30	12.42	0.051
Height	1	154.35	154.35	8.52	0.091
Cleared	1	31.61	31.61	2.75	0.236
Region×Position	1	26.57	26.57	2.96	0.201
Region×Height	1	45.80	45.80	2.52	0.244
Region×Cleared	1	5.68	5.68	0.50	0.552
Position×Height	1	27.24	27.24	4.21	0.043
Position×Cleared	1	0.13	0.13	0.02	0.887
Height×Cleared	1	0.23	0.23	0.04	0.850
Position×Loch(Region)	2	18.79	9.39	1.45	0.239
Height×Loch(Region)	2	39.00	19.50	3.01	0.053
Cleared×Loch(Region)	2	23.17	11.59	1.79	0.172
Region×Position×Height	1	0.25	0.25	0.04	0.846
Region×Position×Cleared	1	15.65	15.65	2.42	0.123
Region×Height×Cleared	1	0.08	0.08	0.01	0.912
Position×Height×Cleared	1	0.46	0.46	0.07	0.790
Residual	113	731.44	6.47		
Total	135				

Appendix 2.11 Nested ANOVA of *P. vulgata* abundance during August 2003 and March 2004.

	d.f.	SS	MS	F ratio	P value
August 2003					
Region	1	2.13	2.13	0.07	0.813
Loch(Region)	2	89.23	44.62	2.96	0.362
Position	1	40.53	40.53	9.77	0.011
Height	1	87.93	87.93	5.21	0.130
Cleared	1	63.24	63.24	15.85	0.003
Region×Position	1	4.30	4.30	1.18	0.331
Region×Height	1	5.30	5.30	0.36	0.595
Region×Cleared	1	0.24	0.24	0.06	0.816
Position×Height	1	3.27	3.27	0.57	0.454
Position×Cleared	1	0.07	0.07	0.01	0.914
Height×Cleared	1	5.99	5.99	1.04	0.311
Position×Loch(Region)	2	6.12	3.06	0.53	0.591
Height×Loch(Region)	2	40.51	20.26	3.51	0.034
Cleared×Loch(Region)	2	5.83	2.91	0.50	0.605
Region×Position×Cleared	1	2.65	2.65	0.46	0.500
Region×Height×Cleared	1	1.98	1.98	0.34	0.559
Position×Height×Cleared	1	0.75	0.75	0.13	0.719
Residual	86	496.62	5.78		
Total	107				
March 2004					
Region	1	49.45	49.45	0.40	0.640
Loch(Region)	1	119.97	119.97	2.11	0.290
Position	1	11.44	11.44	0.79	0.547
Height	1	80.31	80.31	2.74	0.352
Cleared	1	40.99	40.99	1.31	0.433
Region×Position	1	0.20	0.20	0.01	0.927
Region×Height	1	20.08	20.08	0.68	0.563
Region×Cleared	1	5.39	5.39	0.17	0.741
Position×Cleared	1	<0.01	<0.01	<0.01	0.996
Height×Cleared	1	8.24	8.24	1.09	0.301
Position×Loch(Region)	1	13.94	13.94	1.84	0.180
Height×Loch(Region)	1	28.13	28.13	3.72	0.059
Cleared×Loch(Region)	1	43.39	43.39	5.74	0.020
Region×Position×Cleared	1	4.51	4.51	0.60	0.443
Region×Height×Cleared	1	11.77	11.77	1.56	0.217
Residual	57	431.16	7.56		
Total	72				

Appendix 2.12 Nested ANOVA of *P. vulgata* abundance during September 2004 and March 2005.

	d.f.	SS	MS	F ratio	P value
September 2004					
Region	1	4.02	4.02	0.52	0.518
Loch(Region)	2	25.22	12.61	0.78	0.579
Position	1	11.16	11.16	0.61	0.515
Height	1	28.74	28.74	8.35	0.005
Cleared	1	3.29	3.29	1.28	0.276
Region×Position	1	3.68	3.68	0.20	0.696
Region×Height	1	0.85	0.85	0.25	0.621
Region×Cleared	1	27.87	27.87	10.84	0.005
Position×Cleared	1	0.31	0.31	0.09	0.765
Height×Cleared	1	0.56	0.56	0.16	0.689
Position×Loch(Region)	2	37.39	18.70	5.43	0.006
Cleared×Loch(Region)	2	3.49	1.74	0.51	0.605
Region×Position×Cleared	1	1.58	1.58	0.46	0.501
Region×Height×Cleared	1	15.78	15.78	4.58	0.036
Residual	68	234.15	3.44		
Total	85				
March 2005					
Region	1	13.10	13.10	0.27	0.648
Loch(Region)	2	228.33	114.17	2.26	0.210
Position	1	74.68	74.68	4.99	0.128
Height	1	45.32	45.32	3.73	0.139
Cleared	1	4.22	4.22	0.40	0.561
Region×Position	1	33.83	33.83	2.21	0.251
Region×Height	1	56.88	56.88	4.74	0.106
Region×Cleared	1	1.14	1.14	0.10	0.762
Position×Height	1	61.91	61.91	13.13	0.001
Position×Cleared	1	2.72	2.72	0.58	0.450
Height×Cleared	1	<0.01	<0.01	<0.01	0.994
Position×Loch(Region)	2	41.05	20.53	4.35	0.016
Height×Loch(Region)	2	46.55	23.28	4.94	0.010
Cleared×Loch(Region)	2	49.47	24.74	5.25	0.007
Region×Position×Cleared	1	6.11	6.11	1.30	0.259
Region×Height×Cleared	1	0.29	0.29	0.06	0.806
Position×Height×Cleared	1	0.21	0.21	0.05	0.832
Residual	74	348.83	4.71		
Total	95				

Appendix 2.13 Results of the summary statistics for *L. littorea* abundance using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
Region	1	481.04	481.04	1.55	0.339
Loch(Region)	2	724.73	362.37	4.08	0.166
Position	1	9.13	9.13	0.13	0.748
Height	1	28.85	28.85	2.33	0.258
Cleared	1	4.76	4.76	1.01	0.418
Region×Position	1	7.43	7.43	0.11	0.772
Region×Height	1	33.33	33.33	2.69	0.234
Region×Cleared	1	3.45	3.45	0.73	0.479
Position×Height	1	4.69	4.69	1.17	0.282
Position×Cleared	1	1.10	1.10	0.27	0.601
Height×Cleared	1	1.30	1.30	0.32	0.571
Position×Loch(Region)	2	157.58	78.79	19.61	<0.001
Height×Loch(Region)	2	26.72	13.36	3.33	0.039
Cleared×Loch(Region)	2	9.50	4.75	1.18	0.310
Region×Position×Height	1	3.79	3.79	0.94	0.334
Region×Position×Cleared	1	1.35	1.35	0.34	0.564
Region×Height×Cleared	1	0.81	0.81	0.20	0.654
Position×Height×Cleared	1	1.04	1.04	0.26	0.612
Residual	113	453.95	4.02		
Total	135				

Appendix 2.14 Nested ANOVA of *L. littorea* abundance during August 2003 and March 2004 (* denominator of the F test is zero).

	d.f.	SS	MS	F ratio	P value
August 2003					
Region	1	467.96	467.96	1.31	0.370
Loch(Region)	2	1116.53	558.27	22.41	0.047
Position	1	0.59	0.59	0.03	0.865
Height	1	68.99	68.99	7.68	0.070
Cleared	1	16.55	16.55	2.68	0.153
Region×Position	1	24.95	24.95	1.23	0.368
Region×Height	1	8.81	8.81	1.02	0.367
Region×Cleared	1	2.20	2.20	0.35	0.569
Position×Height	1	22.33	22.33	3.20	0.077
Position×Cleared	1	25.68	25.68	3.68	0.058
Height×Cleared	1	3.40	3.40	0.49	0.487
Position×Loch(Region)	2	47.83	23.91	3.43	0.037
Height×Loch(Region)	2	19.19	9.59	1.38	0.258
Cleared×Loch(Region)	2	11.38	5.69	0.82	0.445
Region×Position×Cleared	1	0.10	0.10	0.01	0.903
Region×Height×Cleared	1	13.24	13.24	1.90	0.172
Position×Height×Cleared	1	26.15	26.15	3.75	0.056
Residual	86	599.39	6.97		
Total	107				
March 2004					
Region	1	984.61	984.61	*	
Loch(Region)	1	0.24	0.24	*	
Position	1	0.17	0.17	*	
Height	1	145.86	145.86	*	
Cleared	1	18.29	18.29	2.50	0.119
Region×Position	1	2.56	2.56	*	
Region×Height	1	195.10	195.10	*	
Region×Cleared	1	22.20	22.20	3.03	0.087
Position×Cleared	1	3.38	3.38	0.16	0.690
Height×Cleared	1	38.39	38.39	1.82	0.182
Position×Loch(Region)	1	1.01	1.01	0.05	0.827
Height×Loch(Region)	1	0.03	0.03	<0.01	0.969
Cleared×Loch(Region)	1	0.35	0.35	0.02	0.897
Region×Position×Cleared	1	0.19	0.19	0.01	0.925
Region×Height×Cleared	1	22.33	22.33	1.06	0.307
Residual	57	1199.36	21.04		
Total	72				

Appendix 2.15 Nested ANOVA of *L. littorea* abundance during September 2004 and March 2005.

	d.f.	SS	MS	F ratio	P value
September 2004					
Region	1	305.81	305.81	2.30	0.257
Loch(Region)	2	535.70	267.85	5.05	0.153
Position	1	7.85	7.85	0.16	0.727
Height	1	31.33	31.33	2.46	0.122
Cleared	1	7.93	7.93	0.52	0.498
Region×Position	1	0.89	0.89	0.02	0.905
Region×Height	1	32.73	32.73	2.57	0.114
Region×Cleared	1	18.99	18.99	1.26	0.307
Position×Cleared	1	0.03	0.03	<0.01	0.962
Height×Cleared	1	7.18	7.18	0.56	0.456
Position×Loch(Region)	2	100.31	50.15	3.93	0.024
Cleared×Loch(Region)	2	34.73	17.36	1.36	0.263
Region×Position×Cleared	1	3.27	3.27	0.26	0.614
Region×Height×Cleared	1	12.82	12.82	1.00	0.320
Residual	68	867.34	12.76		
Total	85				
March 2005					
Region	1	31.42	31.42	1.27	0.329
Loch(Region)	2	93.43	46.72	1.04	0.476
Position	1	16.72	16.72	0.45	0.558
Height	1	1.22	1.22	0.11	0.752
Cleared	1	29.33	29.33	2.79	0.112
Region×Position	1	1.04	1.04	0.03	0.881
Region×Height	1	5.77	5.77	0.50	0.496
Region×Cleared	1	1.91	1.91	0.18	0.676
Position×Height	1	34.18	34.18	3.32	0.073
Position×Cleared	1	23.01	23.01	2.23	0.139
Height×Cleared	1	22.96	22.96	2.23	0.140
Position×Loch(Region)	2	102.52	51.26	4.98	0.009
Height×Loch(Region)	2	26.75	13.38	1.30	0.279
Cleared×Loch(Region)	2	22.12	11.06	1.07	0.347
Region×Position×Cleared	1	0.80	0.80	0.08	0.781
Region×Height×Cleared	1	0.83	0.83	0.08	0.777
Position×Height×Cleared	1	36.59	36.59	3.55	0.063
Residual	74	762.09	10.30		
Total	95				

Appendix 2.16 Results of the summary statistics for *Littorina* species abundance using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
Region	1	47.95	47.95	0.72	0.486
Loch(Region)	2	156.29	78.15	12.46	0.076
Position	1	5.79	5.79	1.56	0.324
Height	1	5.26	5.26	9.23	0.037
Cleared	1	5.39	5.39	0.97	0.427
Region×Position	1	0.67	0.67	0.18	0.707
Region×Height	1	3.32	3.32	5.85	0.072
Region×Cleared	1	3.52	3.52	0.64	0.506
Position×Height	1	0.01	0.01	<0.01	0.952
Position×Cleared	1	2.89	2.89	1.75	0.188
Height×Cleared	1	3.47	3.47	2.10	0.150
Position×Loch(Region)	2	8.15	4.07	2.47	0.089
Height×Loch(Region)	2	0.88	0.44	0.27	0.765
Cleared×Loch(Region)	2	11.23	5.61	3.40	0.037
Region×Position×Height	1	1.71	1.71	1.04	0.311
Region×Position×Cleared	1	0.66	0.66	0.40	0.528
Region×Height×Cleared	1	2.04	2.04	1.23	0.269
Position×Height×Cleared	1	0.85	0.85	0.52	0.474
Residual	113	186.39	1.65		
Total	135				

Appendix 2.17 Nested ANOVA of *Littorina* species abundance during August 2003 and March 2004.

	d.f.	SS	MS	F ratio	P value
August 2003					
Region	1	52.30	52.30	1.01	0.413
Loch(Region)	2	155.87	77.94	1.82	0.371
Position	1	52.59	52.59	1.73	0.299
Height	1	0.93	0.93	0.13	0.742
Cleared	1	0.21	0.21	0.04	0.839
Region×Position	1	6.56	6.56	0.17	0.714
Region×Height	1	20.80	20.80	2.90	0.151
Region×Cleared	1	0.40	0.40	0.08	0.784
Position×Height	1	1.39	1.39	0.20	0.654
Position×Cleared	1	8.64	8.64	1.26	0.264
Height×Cleared	1	9.55	9.55	1.40	0.240
Position×Loch(Region)	2	92.24	46.12	6.75	0.002
Height×Loch(Region)	2	14.72	7.36	1.08	0.345
Cleared×Loch(Region)	2	7.27	3.64	0.53	0.589
Region×Position×Cleared	1	4.49	4.49	0.66	0.420
Region×Height×Cleared	1	3.53	3.53	0.52	0.474
Position×Height×Cleared	1	0.75	0.75	0.11	0.741
Residual	86	587.72	6.83		
Total	107				
March 2004					
Region	1	0.43	0.43	0.01	0.950
Loch(Region)	1	69.16	69.16	0.71	0.529
Position	1	3.89	3.89	0.04	0.870
Height	1	0.35	0.35	0.27	0.727
Cleared	1	45.74	45.74	2.09	0.358
Region×Position	1	20.99	20.99	0.23	0.715
Region×Height	1	1.68	1.68	1.28	0.527
Region×Cleared	1	0.01	0.01	<0.01	0.987
Position×Cleared	1	7.87	7.87	1.51	0.224
Height×Cleared	1	12.50	12.50	2.40	0.127
Position×Loch(Region)	1	84.20	84.20	16.18	<0.001
Height×Loch(Region)	1	1.53	1.53	0.29	0.590
Cleared×Loch(Region)	1	30.41	30.41	5.84	0.019
Region×Position×Cleared	1	42.32	42.32	8.13	0.006
Region×Height×Cleared	1	2.71	2.71	0.52	0.474
Residual	57	296.70	5.21		
Total	72				

Appendix 2.18 Nested ANOVA of *Littorina* species abundance during September 2004 and March 2005.

	d.f.	SS	MS	F ratio	P value
September 2004					
Region	1	8.19	8.19	0.92	0.419
Loch(Region)	2	33.29	16.64	2.27	0.286
Position	1	0.08	0.08	0.02	0.890
Height	1	0.69	0.69	0.36	0.552
Cleared	1	4.62	4.62	1.16	0.352
Region×Position	1	0.13	0.13	0.04	0.857
Region×Height	1	8.71	8.71	4.48	0.038
Region×Cleared	1	0.17	0.17	0.04	0.850
Position×Cleared	1	5.23	5.23	2.70	0.105
Height×Cleared	1	5.90	5.90	3.04	0.086
Position×Loch(Region)	2	6.63	3.31	1.71	0.189
Cleared×Loch(Region)	2	11.89	5.94	3.06	0.053
Region×Position×Cleared	1	0.62	0.62	0.32	0.574
Region×Height×Cleared	1	0.07	0.07	0.04	0.852
Residual	68	132.00	1.94		
Total	85				
March 2005					
Region	1	12.92	12.92	0.22	0.676
Loch(Region)	2	264.26	132.13	3.63	0.178
Position	1	15.29	15.29	1.48	0.284
Height	1	0.05	0.05	<0.01	0.958
Cleared	1	21.30	21.30	1.48	0.261
Region×Position	1	1.05	1.05	0.10	0.765
Region×Height	1	7.31	7.31	0.47	0.522
Region×Cleared	1	0.28	0.28	0.02	0.893
Position×Height	1	42.65	42.65	4.30	0.042
Position×Cleared	1	47.87	47.87	4.83	0.031
Height×Cleared	1	13.34	13.34	1.35	0.250
Position×Loch(Region)	2	21.22	10.61	1.07	0.348
Height×Loch(Region)	2	48.55	24.27	2.45	0.093
Cleared×Loch(Region)	2	50.27	25.13	2.54	0.086
Region×Position×Cleared	1	<0.01	<0.01	<0.01	0.992
Region×Height×Cleared	1	0.33	0.33	0.03	0.855
Position×Height×Cleared	1	28.53	28.53	2.88	0.094
Residual	74	733.58	9.91		
Total	95				

Appendix 2.19 Results of the summary statistics for density of *Semibalanus balanoides* using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
Region	1	35.427	35.427	2.18	0.242
Loch(Region)	2	40.695	20.348	0.39	0.707
Position	1	17.398	17.398	0.60	0.505
Height	1	1.692	1.692	0.14	0.736
Cleared	1	1.815	1.815	0.13	0.752
Region×Position	1	1.577	1.577	0.05	0.840
Region×Height	1	6.443	6.443	0.55	0.505
Region×Cleared	1	6.169	6.169	0.45	0.552
Position×Height	1	27.538	27.538	3.52	0.064
Position×Cleared	1	4.116	4.116	0.53	0.470
Height×Cleared	1	2.933	2.933	0.37	0.542
Position×Loch(Region)	2	79.590	39.795	5.08	0.008
Height×Loch(Region)	2	27.842	13.921	1.78	0.175
Cleared×Loch(Region)	2	32.087	16.044	2.05	0.135
Region×Height×Cleared	1	6.314	6.314	0.81	0.372
Position×Height×Cleared	1	2.782	2.782	0.36	0.553
Residual	85	665.585	7.830		
Total	105				

Appendix 2.20 Nested ANOVA of *S. balanoides* density during August 2003 and March 2004 (* denominator of the F test is zero).

	d.f.	SS	MS	F ratio	P value
August 2003					
Region	1	30.568	30.568	6.73	0.019
Loch(Region)	2	4.674	2.337	0.03	0.971
Position	1	16.565	16.565	4.15	0.053
Height	1	46.484	46.484	0.78	0.465
Cleared	1	21.351	21.351	2.51	0.176
Region×Position	1	0.200	0.200	0.05	0.823
Region×Height	1	14.652	14.652	0.26	0.653
Region×Cleared	1	3.936	3.936	0.46	0.526
Position×Height	1	12.119	12.119	1.43	0.236
Position×Cleared	1	16.684	16.684	1.97	0.165
Height×Cleared	1	14.509	14.509	1.71	0.195
Position×Loch(Region)	2	3.298	1.649	0.19	0.824
Height×Loch(Region)	2	164.313	82.156	9.69	<0.001
Cleared×Loch(Region)	2	17.047	8.524	1.01	0.371
Region×Position×Cleared	1	66.392	66.392	7.83	0.007
Region×Height×Cleared	1	3.843	3.843	0.45	0.503
Position×Height×Cleared	1	6.861	6.861	0.81	0.371
Residual	72	610.360	8.477		
Total	93				
March 2004					
Region	1	4.027	4.027	*	
Loch(Region)	1	0.082	0.082	0.02	0.921
Position	1	7.861	7.861	1.61	0.425
Height	1	2.927	2.927	4.28	0.212
Cleared	1	0.007	0.007	0.02	0.897
Region×Position	1	4.885	4.885	1.00	0.500
Region×Height	1	20.881	20.881	30.57	0.054
Region×Cleared	1	0.004	0.004	0.01	0.925
Position×Cleared	1	0.182	0.182	0.17	0.682
Height×Cleared	1	1.560	1.560	1.47	0.235
Position×Loch(Region)	1	4.889	4.889	4.60	0.041
Height×Loch(Region)	1	0.629	0.629	0.59	0.448
Cleared×Loch(Region)	1	0.168	0.168	0.16	0.694
Region×Position×Cleared	1	1.356	1.356	1.28	0.268
Region×Height×Cleared	1	0.451	0.451	0.42	0.520
Residual	29	30.831	1.063		
Total	44				

Appendix 2.21 Nested ANOVA of *S. balanoides* density during September 2004 and March 2005.

	d.f.	SS	MS	F ratio	P value
September 2004					
Region	1	17.391	17.391	6.41	0.017
Loch(Region)	2	4.780	2.390	1.30	0.578
Position	1	16.926	16.926	8.02	0.024
Height	1	3.921	3.921	1.40	0.243
Cleared	1	0.420	0.420	0.14	0.719
Region×Position	1	0.668	0.668	0.37	0.591
Region×Height	1	0.366	0.366	0.13	0.719
Region×Cleared	1	1.111	1.111	0.38	0.586
Position×Height	1	37.898	37.898	13.51	0.001
Position×Cleared	1	0.010	0.010	<0.01	0.953
Height×Cleared	1	1.546	1.546	0.55	0.461
Position×Loch(Region)	2	3.422	1.711	0.61	0.547
Cleared×Loch(Region)	2	5.909	2.955	1.05	0.356
Region×Position×Cleared	1	5.401	5.401	1.93	0.171
Position×Height×Cleared	1	1.628	1.628	0.58	0.450
Residual	50	140.279	2.806		
Total	68				
March 2005					
Region	1	2.239	2.239	0.24	0.668
Loch(Region)	2	26.459	13.230	5.30	0.401
Position	1	3.735	3.735	0.78	0.445
Height	1	2.198	2.198	3.48	0.069
Cleared	1	1.855	1.855	1.38	0.246
Region×Position	1	0.554	0.554	0.09	0.793
Region×Height	1	4.723	4.723	4.27	0.044
Region×Cleared	1	0.753	0.753	0.56	0.458
Position×Height	1	0.568	0.568	0.25	0.620
Position×Cleared	1	4.496	4.496	1.97	0.166
Height×Cleared	1	0.210	0.210	0.09	0.762
Position×Loch(Region)	2	12.312	6.156	2.70	0.077
Height×Loch(Region)	2	0.225	0.113	0.05	0.952
Cleared×Loch(Region)	2	0.666	0.333	0.15	0.864
Region×Position×Cleared	1	7.632	7.632	3.35	0.073
Region×Height×Cleared	1	0.718	0.718	0.32	0.577
Position×Height×Cleared	1	0.880	0.880	0.39	0.537
Residual	52	118.492	2.279		
Total	73				

Appendix 2.22 Results of the summary statistics examining *Semibalanus balanoides* lengths from two settlement periods, established and 2003 using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
Established population					
Region	1	8.9626	8.9626	88.33	<0.001
Loch(Region)	2	0.0495	0.0247	0.01	0.992
Position	1	3.5265	3.5265	1.70	0.315
Height	1	0.0840	0.0840	0.40	0.556
Region×Position	1	1.1718	1.1718	0.58	0.520
Region×Height	1	0.7095	0.7095	3.39	0.124
Position×Height	1	0.0045	0.0045	0.02	0.892
Position×Loch(Region)	2	5.7187	2.8594	11.88	<0.001
Height×Loch(Region)	2	0.3886	0.1943	0.81	0.449
Residual	87	20.9398	0.2407		
Total	99				
2003 settlement					
Region	1	0.8765	0.8765	0.56	0.527
Loch(Region)	2	4.4684	2.2342	1.23	0.409
Position	1	0.6722	0.6722	0.67	0.491
Height	1	1.3710	1.3710	4.87	0.122
Cleared	1	0.3116	0.3116	1.02	0.385
Region×Position	1	0.1705	0.1705	0.16	0.727
Region×Height	1	0.0104	0.0104	0.04	0.855
Region×Cleared	1	0.0904	0.0904	0.30	0.620
Position×Height	1	0.0959	0.0959	0.63	0.430
Position×Cleared	1	0.5031	0.5031	3.29	0.073
Height×Cleared	1	0.1122	0.1122	0.73	0.394
Position×Loch(Region)	2	2.9000	1.4500	9.49	<0.001
Height×Loch(Region)	2	0.6610	0.3305	2.16	0.121
Cleared×Loch(Region)	2	0.8216	0.4108	2.69	0.074
Region×Position×Cleared	1	0.0370	0.0370	0.24	0.624
Region×Height×Cleared	1	0.1235	0.1235	0.81	0.371
Position×Height×Cleared	1	0.0696	0.0696	0.46	0.502
Residual	82	12.5262	0.1528		
Total	103				

Appendix 2.23 Results of the summary statistics examining *Semibalanus balanoides* lengths from two settlement periods, 2004 and 2005 using a nested ANOVA design.

	d.f.	SS	MS	F ratio	P value
2004 settlement					
Region	1	0.0012	0.0012	0.01	0.938
Loch(Region)	2	0.7740	0.3870	0.43	0.703
Position	1	0.3385	0.3385	0.49	0.546
Height	1	0.0005	0.0005	<0.01	0.954
Cleared	1	0.1063	0.1063	0.99	0.347
Region×Position	1	<0.0001	<0.0001	<0.01	0.996
Region×Height	1	0.0704	0.0704	0.47	0.498
Region×Cleared	1	0.2244	0.2244	2.43	0.203
Position×Height	1	0.0694	0.0694	0.46	0.501
Position×Cleared	1	0.0170	0.0170	0.11	0.739
Height×Cleared	1	0.0075	0.0075	0.05	0.825
Position×Loch(Region)	2	1.9372	0.9686	6.40	0.003
Cleared×Loch(Region)	2	0.1630	0.0815	0.54	0.587
Region×Position×Cleared	1	0.0565	0.0565	0.37	0.544
Position×Height×Cleared	1	0.0061	0.0061	0.04	0.842
Residual	51	7.7200	0.1514		
Total	69				
2005 settlement					
Region	1	0.3288	0.3288	1.03	0.414
Loch(Region)	2	1.3976	0.6988	2.97	0.234
Position	1	0.1464	0.1464	1.41	0.346
Height	1	<0.0001	<0.0001	<0.01	0.982
Cleared	1	0.0438	0.0438	2.28	0.204
Region×Position	1	0.0001	0.0001	<0.01	0.987
Region×Height	1	0.2642	0.2642	23.35	<0.001
Region×Cleared	1	0.0011	0.0011	0.04	0.852
Position×Height	1	0.1091	0.1091	9.64	0.003
Position×Cleared	1	0.0718	0.0718	6.35	0.015
Height×Cleared	1	0.0259	0.0259	2.29	0.138
Position×Loch(Region)	2	0.3976	0.1988	17.57	<0.001
Cleared×Loch(Region)	2	0.0552	0.0276	2.44	0.099
Region×Position×Cleared	1	0.0287	0.0287	2.54	0.118
Region×Height×Cleared	1	0.0003	0.0003	0.03	0.872
Position×Height×Cleared	1	0.0398	0.0398	3.51	0.068
Residual	44	0.4979	0.0113		
Total	63				

Appendix 2.24 Results of the summary statistics and three additional months (August 2003, September 2004, and March 2005) examining the density of *Chthamalus montagui*.

	d.f.	SS	MS	F ratio	P value
Summary					
Region	1	3.9892	3.9892	0.34	0.621
Loch(Region)	2	16.6569	8.3284	2.67	0.253
Position	1	1.0287	1.0287	1.05	0.315
Cleared	1	1.0291	1.0291	0.25	0.669
Region×Position	1	0.0376	0.0376	0.04	0.846
Region×Cleared	1	3.9288	3.9288	0.96	0.437
Position×Cleared	1	0.5433	0.5433	0.55	0.463
Cleared×Loch(Region)	2	7.3353	3.6676	3.74	0.038
Residual	25	24.4914	0.9797		
Total	35				
August 2003					
Region	1	0.022	0.022	0.05	0.861
Loch(Region)	2	1.038	0.519	0.66	0.535
Position	1	1.343	1.343	1.71	0.216
Cleared	1	2.939	2.939	3.74	0.077
Residual	12	9.434	0.786		
Total	17				
September 2004					
Region	1	3.488	3.488	0.35	0.617
Loch(Region)	2	19.011	9.505	3.10	0.225
Position	1	1.087	1.087	0.77	0.392
Cleared	1	0.013	0.013	<0.01	0.955
Region×Position	1	0.110	0.110	0.08	0.783
Region×Cleared	1	4.767	4.767	1.49	0.340
Position×Cleared	1	0.441	0.441	0.31	0.583
Cleared×Loch(Region)	2	6.641	3.320	2.36	0.126
Residual	16	22.494	1.406		
Total	26				
March 2005					
Region	1	5.753	5.753	0.68	0.487
Loch(Region)	2	22.502	11.251	5.94	0.010
Position	1	0.202	0.202	0.11	0.748
Cleared	1	1.703	1.703	0.90	0.356
Region×Cleared	1	2.715	2.715	1.43	0.247
Residual	18	34.114	1.895		
Total	24				

Appendix 2.25 Results of the summary statistics for *Chthamalus montagui* lengths of the established population and the three settlements of 2003, 2004, and 2005.

	d.f.	SS	MS	F ratio	P value
Established					
Region	1	0.5083	0.5082	43.41	0.352
Loch(Region)	2	0.0471	0.0236	0.26	0.775
Position	1	0.2147	0.2147	2.35	0.137
Residual	26	2.3754	0.0914		
Total	30				
2003					
Region	1	0.0037	0.0037	0.01	0.925
Loch(Region)	2	0.6886	0.3443	0.78	0.475
Position	1	0.0250	0.0250	0.06	0.815
Cleared	1	0.1821	0.1821	0.41	0.530
Region×Position	1	0.0331	0.0331	0.07	0.788
Region×Cleared	1	0.0066	0.0066	0.01	0.905
Position×Cleared	1	0.0708	0.0708	0.16	0.694
Residual	19	8.4397	0.4442		
Total	27				
2004					
Region	1	0.0976	0.0976	0.22	0.688
Loch(Region)	2	0.8344	0.4172	1.81	0.205
Position	1	<0.0001	<0.0001	<0.01	0.990
Cleared	1	0.0111	0.0111	0.05	0.830
Region×Cleared	1	0.0114	0.0114	0.05	0.828
Position×Cleared	1	0.1351	0.1351	0.59	0.458
Residual	12	2.7617	0.2301		
Total	19				

Appendix 2.26 Nested ANOVA results of monthly analysis of *C. montagui* lengths from the established population.

	d.f.	SS	MS	F ratio	P value
August 2003					
Region	1	4.7134	4.7134	29.17	<0.001
Loch(Region)	2	0.1442	0.0721	0.20	0.816
Position	1	1.7746	1.7746	5.00	0.027
Residual	163	57.8628	0.3550		
Total	167				
September 2004					
Region	1	3.5146	3.5146	8.56	0.010
Loch(Region)	2	0.9148	0.4574	1.18	0.312
Position	1	0.1556	0.1556	0.40	0.528
Residual	138	53.6797	0.3890		
Total	142				
March 2005					
Region	1	0.5060	0.5060	0.81	0.404
Loch(Region)	2	2.4894	1.2447	3.48	0.033
Position	1	4.7233	4.7233	13.20	<0.001
Residual	148	52.9683	0.3579		
Total	152				

Appendix 2.27 Nested ANOVA results of monthly analysis of *C. montagui* lengths from the 2003 settlement.

	d.f.	SS	MS	F ratio	P value
September 2004					
Region	1	0.05404	0.05404	0.25	0.647
Loch(Region)	2	1.45274	0.72637	10.32	<0.001
Position	1	0.07850	0.07850	1.12	0.293
Cleared	1	0.39170	0.39170	5.57	0.020
Region×Position	1	0.00693	0.00693	0.10	0.754
Region×Cleared	1	0.03052	0.03052	0.43	0.511
Position×Cleared	1	0.16971	0.16971	2.41	0.123
Residual	140	9.84974	0.07036		
Total	148				
March 2005					
Region	1	0.00206	0.00206	0.03	0.877
Loch(Region)	2	0.40211	0.20106	4.07	0.019
Position	1	1.53704	1.53704	31.14	<0.001
Cleared	1	0.01527	0.01527	0.31	0.579
Region×Cleared	1	0.17755	0.17755	3.60	0.060
Position×Cleared	1	0.55257	0.55257	11.19	0.001
Residual	130	6.41735	0.04936		
Total	137				

Appendix 3

Appendix 3.1 ANCOVA results for *M. edulis* growth over 203 days from initial length. Results for small (<30 mm shell length), medium (≥30 mm, ≤40 mm), and large (>40 mm) mussels are shown.

	d.f.	SS	MS	F ratio	P value
Small					
Treatment	5	5.45	21.85	22.09	<0.001
Initial	1	28.34	261.45	264.34	<0.001
Treatment×Initial	5	5.26	1.05	1.06	0.397
Residual	35	34.62	0.99		
Total	46				
Medium					
Treatment	5	11.05	2.80	4.03	0.003
Initial	1	449.21	549.33	791.95	<0.001
Treatment×Initial	5	9.78	1.96	2.82	0.022
Residual	78	54.10	0.69		
Total	89				
Large					
Treatment	5	1.11	15.78	21.26	<0.001
Initial	1	44.96	480.38	646.99	<0.001
Treatment×Initial	5	1.05	0.21	0.28	0.920
Residual	46	34.16	0.74		
Total	57				

Appendix 3.2 ANCOVA results for *M. edulis* growth over 110 days after the initial 203 days from the start of the experiment. Results for small (<30 mm shell length), medium (≥30 mm, ≤40 mm), and large (>40 mm) mussels are shown.

	d.f.	SS	MS	F ratio	P value
Small					
Treatment	4	6.51	3.34	4.48	0.007
Initial	1	18.44	100.97	135.36	<0.001
Treatment×Initial	4	4.63	1.16	1.55	0.218
Residual	25	18.65	0.75		
Total	34				
Medium					
Treatment	4	7.48	29.34	55.76	<0.001
Initial	1	334.34	399.99	760.03	<0.001
Treatment×Initial	4	4.74	1.19	2.25	0.074
Residual	62	32.63	0.53		
Total	71				
Large					
Treatment	4	1.10	10.84	23.58	<0.001
Initial	1	28.66	210.77	458.29	<0.001
Treatment×Initial	4	1.25	0.31	0.68	0.612
Residual	28	12.88	0.46		
Total	37				

Appendix 4

Appendix 4.1 Results of the summary statistics for barnacle cover under differing predation and grazing pressures.

	d.f.	SS	MS	F ratio	P value
Region	1	1109.4	1109.4	0.32	0.627
Loch(Region)	2	6850.1	3425.1	3.34	0.213
Predator	1	295.6	295.6	1.56	0.337
Region×Predator	1	1.2	1.2	0.01	0.943
Predator×Loch(Region)	2	377.8	188.9	3.28	0.085
Grazer	1	3.2	3.2	6.49	0.126
Region×Grazer	1	71.7	71.7	146.70	0.007
Grazer×Loch(Region)	2	1.0	0.5	0.01	0.992
Predator×Grazer	1	616.2	616.2	10.69	0.010
Region×Predator×Grazer	1	70.3	70.3	1.22	0.298
Cleared	1	5836.6	5836.6	6.14	0.132
Region×Cleared	1	98.0	98.0	0.10	0.779
Cleared×Loch(Region)	2	1901.9	951.0	16.49	0.001
Predator×Cleared	1	90.6	90.6	1.57	0.242
Grazer×Cleared	1	17.7	17.7	0.31	0.593
Predator×Grazer×Cleared	1	21.4	21.4	0.37	0.558
Region×Predator×Cleared	1	10.5	10.5	0.18	0.680
Region×Grazer×Cleared	1	0.6	0.6	0.01	0.922
Residual	9	518.9	57.7		
Total	31				

Appendix 4.2 Nested ANOVA of initial barnacle cover and cover one month later under differing predation and grazing pressures.

	d.f.	SS	MS	F ratio	P value
Initial cover					
Region	1	16007.4	16007.4	13.80	0.065
Loch(Region)	2	2330.6	1165.3	0.91	0.622
Predator	1	190.9	190.9	0.09	0.787
Region×Predator	1	1178.3	1178.3	0.59	0.524
Predator×Loch(Region)	2	4042.7	2021.3	5.26	0.008
Grazer	1	79.9	79.9	4.83	0.120
Region×Grazer	1	140.9	140.9	8.51	0.065
Grazer×Loch(Region)	2	27.8	13.9	0.04	0.964
Predator×Grazer	1	1255.2	1255.2	3.27	0.075
Region×Predator×Grazer	1	346.4	346.4	0.90	0.346
Cleared	1	501.2	501.2	25.05	0.021
Region×Cleared	1	988.7	988.7	49.42	0.009
Cleared×Loch(Region)	2	35.3	17.6	0.05	0.955
Predator×Cleared	1	187.6	187.6	0.49	0.487
Grazer×Cleared	1	406.1	406.1	1.06	0.308
Predator×Grazer×Cleared	1	318.3	318.3	0.83	0.366
Region×Predator×Cleared	1	282.5	282.5	0.74	0.394
Region×Grazer×Cleared	1	0.3	0.3	<0.01	0.979
Residual	67	25743.0	384.2		
Total	89				
Cover after one month					
Region	1	199.2	199.2	0.01	0.932
Loch(Region)	2	43305.7	21652.9	6.32	0.167
Predator	1	36.1	36.1	0.39	0.592
Region×Predator	1	110.3	110.3	1.20	0.384
Predator×Loch(Region)	2	181.4	90.7	0.40	0.671
Grazer	1	0.3	0.3	0.01	0.936
Region×Grazer	1	297.2	297.2	8.44	0.090
Grazer×Loch(Region)	2	67.7	33.8	0.15	0.861
Predator×Grazer	1	955.4	955.4	4.22	0.044
Region×Predator×Grazer	1	888.8	888.8	3.93	0.052
Cleared	1	38379.8	38379.8	10.25	0.085
Region×Cleared	1	3773.7	3773.7	1.01	0.421
Cleared×Loch(Region)	2	7535.6	3767.8	16.66	<0.001
Predator×Cleared	1	24.9	24.9	0.11	0.741
Grazer×Cleared	1	55.2	55.2	0.24	0.623
Predator×Grazer×Cleared	1	190.9	190.9	0.84	0.361
Region×Predator×Cleared	1	49.2	49.2	0.22	0.642
Region×Grazer×Cleared	1	118.2	118.2	0.52	0.472
Residual	67	15151.9	226.1		
Total	89				

Appendix 4.3 Nested ANOVA of barnacle cover two and three months after the start of the experiment under differing predation and grazing pressures.

	d.f.	SS	MS	F ratio	P value
Cover after two months					
Region	1	2231.2	2231.2	0.10	0.783
Loch(Region)	2	45680.8	22840.4	3.62	0.208
Predator	1	2228.3	2228.3	4.35	0.172
Region×Predator	1	179.9	179.9	0.35	0.613
Predator×Loch(Region)	2	1028.3	514.2	2.85	0.065
Grazer	1	4.2	4.2	0.17	0.718
Region×Grazer	1	291.9	291.9	11.70	0.065
Grazer×Loch(Region)	2	47.7	23.8	0.13	0.877
Predator×Grazer	1	1628.0	1628.0	9.01	0.004
Region×Predator×Grazer	1	43.8	43.8	0.24	0.624
Cleared	1	20879.7	20879.7	3.42	0.206
Region×Cleared	1	377.0	377.0	0.06	0.827
Cleared×Loch(Region)	2	12298.1	6149.1	34.03	<0.001
Predator×Cleared	1	422.5	422.5	2.34	0.131
Grazer×Cleared	1	236.2	236.2	1.31	0.257
Predator×Grazer×Cleared	1	28.9	28.9	0.16	0.690
Region×Predator×Cleared	1	51.7	51.7	0.29	0.594
Region×Grazer×Cleared	1	71.9	71.9	0.40	0.530
Residual	67	12106.7	180.7		
Total	89				
Cover after three months					
Region	1	3983.5	3983.5	0.29	0.645
Loch(Region)	2	27822.4	13911.2	2.96	0.247
Predator	1	5276.2	5276.2	14.26	0.063
Region×Predator	1	1.3	1.3	<0.01	0.958
Predator×Loch(Region)	2	742.3	371.1	1.72	0.187
Grazer	1	0.3	0.3	<0.01	0.969
Region×Grazer	1	64.2	64.2	0.38	0.601
Grazer×Loch(Region)	2	340.8	170.4	0.79	0.458
Predator×Grazer	1	2810.6	2810.6	13.04	0.001
Region×Predator×Grazer	1	45.2	45.2	0.21	0.648
Cleared	1	19819.4	19819.4	4.32	0.173
Region×Cleared	1	153.1	153.1	0.03	0.872
Cleared×Loch(Region)	2	9224.7	4612.4	21.39	<0.001
Predator×Cleared	1	418.6	418.6	1.94	0.168
Grazer×Cleared	1	481.3	481.3	2.23	0.140
Predator×Grazer×Cleared	1	29.1	29.1	0.13	0.715
Region×Predator×Cleared	1	30.3	30.3	0.14	0.709
Region×Grazer×Cleared	1	46.1	46.1	0.21	0.645
Residual	67	14446.4	215.6		
Total	89				

Appendix 4.4 Results of the summary statistics of empty barnacle tests under differing predation and grazing pressures.

	d.f.	SS	MS	F ratio	P value
Region	1	53.1	53.1	1.73	0.319
Loch(Region)	2	61.2	30.6		
Predator	1	194.0	194.0	28.35	0.034
Region×Predator	1	2.6	2.6	0.38	0.600
Predator×Loch(Region)	2	13.7	6.8	0.55	0.593
Grazer	1	0.9	0.9	0.14	0.744
Region×Grazer	1	0.3	0.3	0.05	0.849
Grazer×Loch(Region)	2	12.5	6.2	0.51	0.619
Predator×Grazer	1	3.2	3.2	0.26	0.625
Region×Predator×Grazer	1	0.8	0.8	0.06	0.808
Cleared	1	515.0	515.0	57.88	0.017
Region×Cleared	1	32.1	32.1	3.61	0.198
Cleared×Loch(Region)	2	17.8	8.9	0.72	0.512
Predator×Cleared	1	151.5	151.5	12.29	0.007
Grazer×Cleared	1	1.3	1.3	0.11	0.753
Predator×Grazer×Cleared	1	1.9	1.9	0.16	0.701
Region×Predator×Cleared	1	0.7	0.7	0.05	0.821
Region×Grazer×Cleared	1	0.4	0.4	0.03	0.866
Residual	9	111.0	12.3		
Total	31				

Appendix 4.5 Nested ANOVA of initial empty barnacle tests and one month after the start of the experiment under differing predation and grazing pressures.

	d.f.	SS	MS	F ratio	P value
Initial					
Region	1	272.59	272.59	0.99	0.424
Loch(Region)	2	551.83	275.91		
Predator	1	9.20	9.20	6.52	0.104
Region×Predator	1	2.13	2.13	1.51	0.325
Predator×Loch(Region)	2	2.59	1.29	0.07	0.929
Grazer	1	1.36	1.36	0.24	0.672
Region×Grazer	1	13.73	13.73	2.41	0.255
Grazer×Loch(Region)	2	11.23	5.61	0.32	0.729
Predator×Grazer	1	4.61	4.61	0.26	0.611
Region×Predator×Grazer	1	5.49	5.49	0.31	0.579
Cleared	1	14.08	14.08	0.91	0.439
Region×Cleared	1	0.56	0.56	0.04	0.866
Cleared×Loch(Region)	2	30.76	15.38	0.87	0.423
Predator×Cleared	1	27.06	27.06	1.53	0.220
Grazer×Cleared	1	0.44	0.44	0.02	0.875
Predator×Grazer×Cleared	1	10.26	10.26	0.58	0.449
Region×Predator×Cleared	1	146.16	146.16	8.27	0.005
Region×Grazer×Cleared	1	7.99	7.99	0.45	0.504
Residual	67	1184.03	17.67		
Total	89				
1st month					
Region	1	185.97	185.97	9.90	0.086
Loch(Region)	2	37.45	18.72	0.24	0.809
Predator	1	724.64	724.64	11.14	0.079
Region×Predator	1	73.25	73.25	1.13	0.399
Predator×Loch(Region)	2	130.69	65.34	2.35	0.103
Grazer	1	25.17	25.17	0.52	0.547
Region×Grazer	1	3.58	3.58	0.07	0.812
Grazer×Loch(Region)	2	97.94	48.97	1.76	0.180
Predator×Grazer	1	2.50	2.50	0.09	0.765
Region×Predator×Grazer	1	0.16	0.16	0.01	0.939
Cleared	1	2616.94	2616.94	136.01	0.007
Region×Cleared	1	184.22	184.22	9.57	0.088
Cleared×Loch(Region)	2	38.37	19.19	0.69	0.505
Predator×Cleared	1	675.48	675.48	24.28	<0.001
Grazer×Cleared	1	13.88	13.88	0.50	0.482
Predator×Grazer×Cleared	1	2.20	2.20	0.08	0.779
Region×Predator×Cleared	1	56.13	56.13	2.02	0.160
Region×Grazer×Cleared	1	0.33	0.33	0.01	0.913
Residual	67	1863.88	27.82		
Total	89				

Appendix 4.6 Nested ANOVA of empty barnacle tests two and three months after the start of the experiment under differing predation and grazing pressures.

	d.f.	SS	MS	F ratio	P value
2nd month					
Region	1	94.58	94.58	1.31	0.371
Loch(Region)	2	145.17	72.58	0.97	0.540
Predator	1	603.69	603.69	29.34	0.031
Region×Predator	1	12.07	12.07	0.59	0.522
Predator×Loch(Region)	2	41.06	20.53	0.75	0.477
Grazer	1	1.28	1.28	0.04	0.853
Region×Grazer	1	0.55	0.55	0.02	0.903
Grazer×Loch(Region)	2	58.43	29.21	1.06	0.351
Predator×Grazer	1	8.27	8.27	0.30	0.585
Region×Predator×Grazer	1	4.99	4.99	0.18	0.671
Cleared	1	2584.43	2584.43	32.45	0.029
Region×Cleared	1	87.22	87.22	1.10	0.405
Cleared×Loch(Region)	2	159.96	79.98	2.91	0.061
Predator×Cleared	1	602.84	602.84	21.96	<0.001
Grazer×Cleared	1	3.40	3.40	0.12	0.726
Predator×Grazer×Cleared	1	7.79	7.79	0.28	0.596
Region×Predator×Cleared	1	10.89	10.89	0.4	0.531
Region×Grazer×Cleared	1	2.10	2.10	0.08	0.783
Residual	67	1839.67	27.46		
Total	89				
3rd month					
Region	1	52.45	52.45	0.45	0.571
Loch(Region)	2	233.90	116.95	0.88	0.507
Predator	1	1342.43	1342.43	17.19	0.053
Region×Predator	1	1.12	1.12	0.01	0.916
Predator×Loch(Region)	2	156.84	78.42	2.60	0.082
Grazer	1	101.50	101.50	2.04	0.289
Region×Grazer	1	0.01	0.01	<0.01	0.989
Grazer×Loch(Region)	2	99.99	49.99	1.66	0.199
Predator×Grazer	1	77.38	77.38	2.56	0.114
Region×Predator×Grazer	1	7.83	7.83	0.26	0.612
Cleared	1	2550.72	2550.72	39.59	0.024
Region×Cleared	1	142.63	142.63	2.21	0.274
Cleared×Loch(Region)	2	129.30	64.65	2.14	0.126
Predator×Cleared	1	1131.16	1131.16	37.45	<0.001
Grazer×Cleared	1	115.91	115.91	3.84	0.054
Predator×Grazer×Cleared	1	27.06	27.06	0.90	0.347
Region×Predator×Cleared	1	12.42	12.42	0.41	0.524
Region×Grazer×Cleared	1	5.31	5.31	0.18	0.676
Residual	67	2023.91	30.21		
Total	89				

Appendix 4.7 Nested ANOVA of algal cover on barnacle tests for summary statistics and one month after the start of the experiment under differing predation and grazing pressures.

	d.f.	SS	MS	F ratio	P value
Summary statistics					
Region	1	3861.9	3861.9	11.42	0.078
Loch(Region)	2	676.6	338.3	0.95	0.483
Predator	1	16.2	16.2	114.68	0.009
Region×Predator	1	30.3	30.3	213.88	0.005
Predator×Loch(Region)	2	0.3	0.1	<0.01	0.995
Grazer	1	37.1	37.1	0.20	0.698
Region×Grazer	1	33.6	33.6	0.18	0.712
Grazer×Loch(Region)	2	370.2	185.1	6.38	0.019
Predator×Grazer	1	1.4	1.4	0.05	0.829
Region×Predator×Grazer	1	0.1	0.1	<0.01	0.954
Cleared	1	3114.7	3114.7	13.52	0.067
Region×Cleared	1	3114.7	3114.7	13.52	0.067
Cleared×Loch(Region)	2	460.7	230.3	7.94	0.010
Predator×Cleared	1	107.4	107.4	3.70	0.087
Grazer×Cleared	1	0.1	0.1	<0.01	0.950
Predator×Grazer×Cleared	1	18.1	18.1	0.62	0.450
Region×Predator×Cleared	1	107.4	107.4	3.70	0.087
Region×Grazer×Cleared	1	0.1	0.1	<0.01	0.950
Residual	9	261.2	29.0		
Total	31				
Cover after one month					
Region	1	11136.1	11136.1	27.27	0.034
Loch(Region)	2	817.7	408.9	0.63	0.675
Predator	1	861.4	861.4	10.46	0.077
Region×Predator	1	919.7	919.7	11.17	0.073
Predator×Loch(Region)	2	161.1	80.5	0.24	0.787
Grazer	1	85.1	85.1	0.10	0.787
Region×Grazer	1	68.1	68.1	0.08	0.808
Grazer×Loch(Region)	2	1796.1	898.0	2.68	0.076
Predator×Grazer	1	301.0	301.0	0.90	0.347
Region×Predator×Grazer	1	336.1	336.1	1.00	0.320
Cleared	1	11007.5	11007.5	31.98	0.029
Region×Cleared	1	10803.1	10803.1	31.39	0.030
Cleared×Loch(Region)	2	688.5	344.2	1.03	0.364
Predator×Cleared	1	688.0	688.0	2.05	0.157
Grazer×Cleared	1	20.0	20.0	0.06	0.808
Predator×Grazer×Cleared	1	291.5	291.5	0.87	0.355
Region×Predator×Cleared	1	740.6	740.6	2.21	0.142
Region×Grazer×Cleared	1	12.2	12.2	0.04	0.850
Residual	67	22475.6	335.5		
Total	89				

Appendix 4.8 Nested ANOVA of algal cover on barnacle tests two and three months after the start of the experiment under differing predation and grazing pressures.

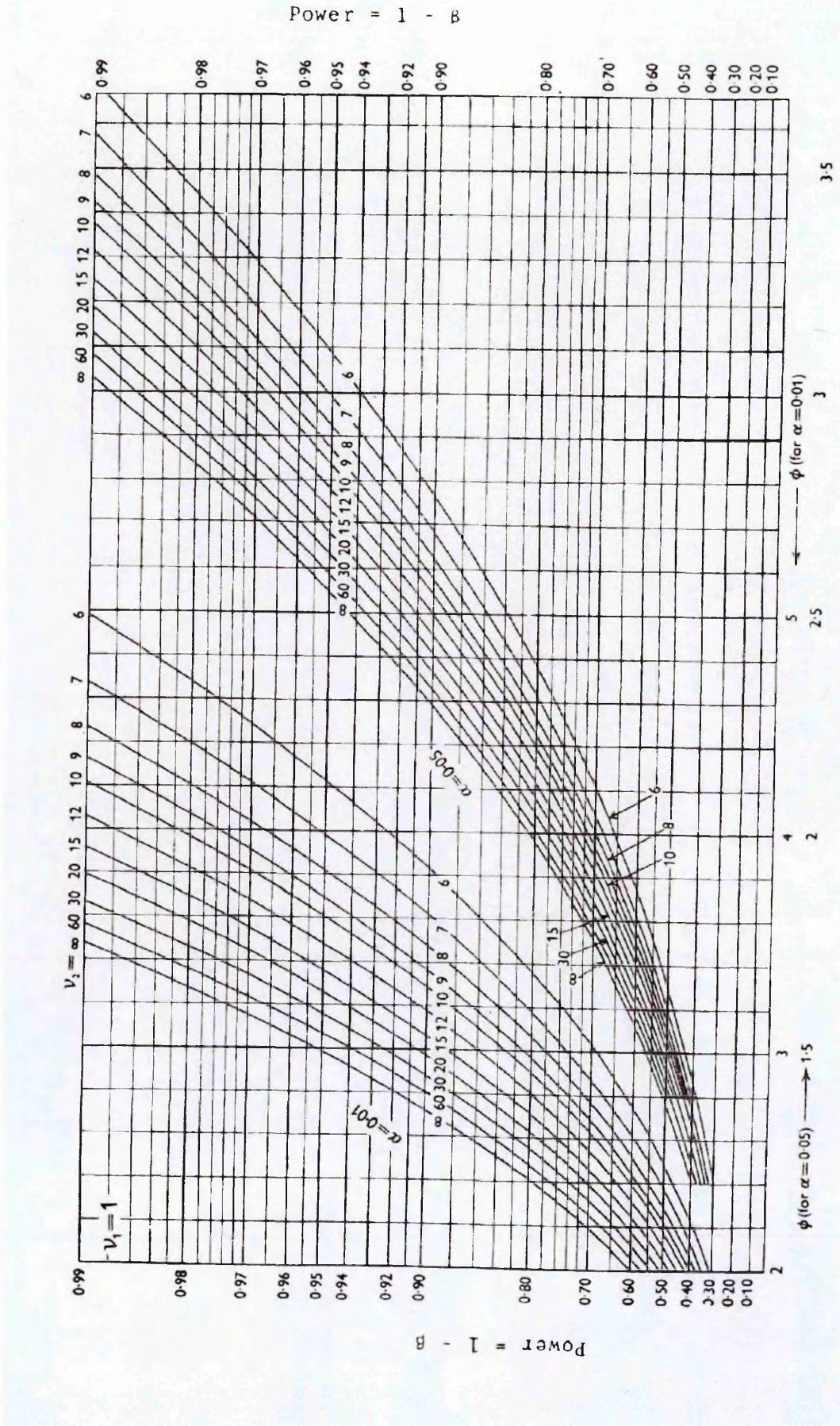
	d.f.	SS	MS	F ratio	P value
Cover after two months					
Region	1	17782.7	17782.7	7.96	0.106
Loch(Region)	2	4494.0	2247.0	1.18	0.467
Predator	1	528.6	528.6	139.42	<0.001
Region×Predator	1	528.6	528.6	139.42	<0.001
Predator×Loch(Region)	2	4.2	2.1	0.01	0.991
Grazer	1	280.8	280.8	0.60	0.520
Region×Grazer	1	280.8	280.8	0.60	0.520
Grazer×Loch(Region)	2	943.5	471.7	1.96	0.149
Predator×Grazer	1	79.5	79.5	0.33	0.568
Region×Predator×Grazer	1	79.5	79.5	0.33	0.568
Cleared	1	16844.2	16844.2	8.80	0.097
Region×Cleared	1	16844.2	16844.2	8.80	0.097
Cleared×Loch(Region)	2	3851.6	1925.8	7.99	0.001
Predator×Cleared	1	599.5	599.5	2.49	0.120
Grazer×Cleared	1	114.5	114.5	0.47	0.493
Predator×Grazer×Cleared	1	28.2	28.2	0.12	0.733
Region×Predator×Cleared	1	599.5	599.5	2.49	0.120
Region×Grazer×Cleared	1	114.5	114.5	0.47	0.493
Residual	67	16151.9	241.1		
Total	89				
Cover after three months					
Region	1	30453.5	30453.5	11.86	0.075
Loch(Region)	2	5165.6	2582.8	1.62	0.374
Predator	1	587.4	587.4	11.92	0.065
Region×Predator	1	238.6	238.6	4.84	0.147
Predator×Loch(Region)	2	94.7	47.3	0.15	0.863
Grazer	1	169.1	169.1	0.15	0.735
Region×Grazer	1	144.7	144.7	0.13	0.754
Grazer×Loch(Region)	2	2257.2	1128.6	3.52	0.035
Predator×Grazer	1	149.6	149.6	0.47	0.497
Region×Predator×Grazer	1	53.5	53.5	0.17	0.684
Cleared	1	17807.4	17807.4	16.88	0.054
Region×Cleared	1	18069.6	18069.6	17.13	0.053
Cleared×Loch(Region)	2	2119.2	1059.6	3.30	0.043
Predator×Cleared	1	85.1	85.1	0.27	0.608
Grazer×Cleared	1	493.4	493.4	1.54	0.219
Predator×Grazer×Cleared	1	198.7	198.7	0.62	0.434
Region×Predator×Cleared	1	67.9	67.9	0.21	0.647
Region×Grazer×Cleared	1	450.7	450.7	1.41	0.240
Residual	67	21483.3	320.6		
Total	89				

Appendix 5

Appendix 5.1 Beaches visited in July 2003 with corresponding co-ordinates and lochs.

Loch Position	Local Name	Latitude	Longitude
Fyne Low	Portavadie	55.87262	-5.31828
Fyne Out1	Ardlamont	55.83587	-5.22513
Riddon Mid	Kinlochruel Boathouse	55.94883	-5.18916
Riddon Low	Fearnoch Bay	55.93925703	-5.18300439
Riddon Out1	StronePoint	55.89740896	-5.08423598
Bute SW	Dunagoil Bay	55.73532	-5.052637
Bute SE	Kilchattan Bay	55.74724758	-5.01511035
Bute W	Kildanavan Point	55.84670934	-5.15667348
Bute NW	Clate Point	55.86724685	-5.1914697
Bute NE	Undraynian point	55.87444321	-5.07441164
Bute E	Kerrycroy	55.81339404	-5.02130239
Long Out1	Cloch	55.93311084	-4.88114834
Striven Out1	Toward	55.86458073	-5.00639895
Striven Low	Port Lamont	55.88989668	-5.04734077
Striven Mid	Inverchaolain	55.93496055	-5.06035519
Long Out2	Innellan	55.89699481	-4.95176545
Fyne Mid	Strathlachlan	56.10082618	-5.21638549
Broom Mid	Ullapool	57.89126608	-5.14248191
Broom Low	Rhue	57.92430636	-5.21985434
Tongue Low	Skullomie	58.52057476	-4.37651351
Tongue Out1	PortVasgo	58.55088363	-4.43246204
Tongue Mid	Causeway	58.499278	-4.448946
Eriboll Mid	An-t-sron	58.48195405	-4.66633952
Eriboll Low	Rispond	58.54830402	-4.6614683
Inchard Out1	Sheigra	58.486375	-5.121648
Inchard Out2	Oldshoremore	58.47612821	-5.08841294
Inchard Low	Kinlochbervie	58.45382245	-5.04992148
Inchard Mid	Achlyness	58.432385	-5.006084
Eriboll Out1	Sangobeg	58.55807296	-4.70363757
Eriboll Out2	Rispond outer	58.55117264	-4.665803
ACHBH Out1	Scourie	58.35331	-5.16776
ACHBH Low	Kylescu Bridge N	58.25743	-5.03745
ACHBH Mid	Unapool	58.35331	-5.16776
ACHBH Out2	Clachtoll	58.18873	-5.33911
Broom Out1	Achnahaird	58.07116	-5.36501
Broom Out2	Badenscallie	57.99972	-5.32663
Torridon Mid	Ardheslaig	57.54752	-5.71088
Torridon Low	Fearnbeg	57.574016	-5.784533
Torridon Out1	Lonbain	57.50906	-5.86608
Carron Out1	Camusteel	57.41097967	-5.82448754
Carron Low	Plockton	57.34177843	-5.64477031
Carron Out2	Drumbuie	57.31938559	-5.70482522
Carron Mid	Slumbay	57.38741387	-5.50397856
Linnhe Out1	Easdale	56.29046682	-5.63406738
Linnhe Out2	Ganavan	56.43785463	-5.47185148
Linnhe Low	Appin	56.58992062	-5.37314544
Linnhe Mid	Corran	56.72126756	-5.23574299
Fyne Out2	Claonaig	55.75190	-5.38382
Kintyre NE	Carradale	55.59275821	-5.46525911
Kintyre E	Campbeltown	55.42461287	-5.58156397
Kintyre S	Southend	55.30747636	-5.66672537
Kintyre W	MachrihanishN	55.47644	-5.71334
Long Mid	Coulport	56.04157	-4.87060
Long Low	Cove	56.00551	-4.85782
Goil Low	Carrick Castle	56.1091282	-4.90598124

Appendix 6



Appendix 6.1 Power and sample size in analysis of variance: v1 = 1 from Zar (1984).